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EDITORIAL COMMITTEE

STEPHEN ALFRED FORBES WILLIAM TRELEASE
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STUDIES ON THE FACTORS CONTROLLING THE RATE OF REGENERATION

BY

CHARLES ZELENY

Contributions from the
Zoological Laboratory of the University of Illinois, No. 73

732172

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INTRODUCTION.

The present studies of the factors controlling rate of regeneration are a continuation of previous work on the subject. An advance in knowledge concerning certain of the factors has made possible an extension of the experimental analysis of others. The present studies are therefore closely related. In fact in several cases a single series of individuals has been of value in connection with more than a single factor. The definite determinations of the effect of level of the cut and of the change in rate during the regeneration cycle have been of particular value.

The precautions taken to meet the demands of the experiments are not discussed in detail because they have already been given in previous papers. The frog tadpoles (when they can be used) are in all respects more suitable than salamander larvae. When collected late in the fall they can be kept at a fairly constant size and the results obtained under these conditions are not complicated with growth phenomena. They have proved to be remarkably uniform in several series. The salamander larvae on the other hand vary in rate of regeneration from day to day. The factors involved in this fluctuation were not discovered and could not be remedied but may be related in some way to the fact that these animals require living active food and the feeding reactions are therefore more complicated than in frog tadpoles and more subject to disturbance.

In regard to certain factors, such as the degree of injury, in which expected differences in rate are slight the writer has felt that he might be biased in making the measurements and in a number of cases this work was therefore delegated to a person who had no preconceptions concerning the result.

In making averages elimination of individual cases is avoided except for a few very aberrant values. Such exceptional values are in every case however included in the tables. In many cases where only slight differences are to be expected several different kinds of comparisons are made so as to bring out the correct relation as completely as possible.

As in the past all data obtained by the writer on the particular factors in question are given. The practice of selective elimination would be dangerous because of the large value of factors not at present under experimental control.

Discussions of the results of other workers are included in the previous papers and need not be repeated here. The principal need at present seems to be an extension of knowledge of these factors by multiplying the number of series of carefully controlled experiments. While it would be interesting to know why a particular series differs from others with respect to a certain factor it is not always possible to discuss the matter profitably in the absence of evidence as to all the factors concerned.

Particular emphasis must be laid on the fact that in connection with some at least of the factors it has been possible to make out very definite quantitative relations. These have been checked up in a number of cases by agreement between separate series of experiments. The success in this direction has made it very probable that with a more accurate control of external conditions there will be a considerable further advance in our knowledge of the factors controlling rate of regeneration.

PART I

THE RATE OF REGENERATION FROM NEW TISSUE COMPARED WITH THAT FROM OLD TISSUE

In comparing first and second regenerations from the same level one of the difficulties that presents itself is the impossibility of making the second cut exactly in the path of the first. This is true not only because of the error in manipulation but also because the old and the new tissues become intermingled and do not retain a distinct dividing line. At the cut surface there is old tissue alone, old and new tissue, or new tissue alone according as the second cut comes inside of the first level, exactly at the level, or outside of it.

The experiments about to be described were devised with a view to the testing of the relative rates from old and from new tissue. Other factors being eliminated, are new cells which are recently produced in a regenerating part able to carry on a repetition of the process more expeditiously than old cells which have not been directly concerned in such a process?

There has been no selective elimination of data. As in former papers of a similar character all the data obtained by the author on the topic at hand are included.

Experiment I Series 3628-3675

Tadpoles of *Rana clamitans* with an average length of 33.4 mm. were used. They were fed just enough to keep them in good condition without much growth. All were collected at one time in a single pool and during the course of the experiment factors apart from the one under investigation were made as nearly alike as possible. This elimination of outside factors was facilitated by subdividing the tadpoles into sets of two each, the two individuals of a set being exactly alike except for the factor under consideration and one being used for regeneration from old tissue and the other for regeneration from new tissue.

Within each set the tail of tadpole 1 was removed at B (Fig. 1) and the tail of tadpole 2 at A. The distance between A and B was 2 or 3 mm. After 21 days of regeneration the second operation on both tadpoles came between A and B and therefore in old tissue in tadpole 1 and in new tissue in tadpole 2. This procedure, insuring approximately the same level in the two cases, is necessary because level of the cut has a great influence upon rate of regeneration. Eleven pairs of individuals were used in the comparison. The precautions taken to eliminate possible error are treated fully elsewhere for similar cases (Zeleny 1909a, 1909b).

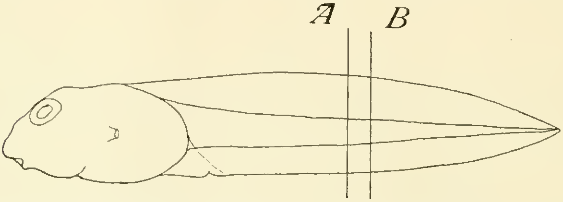

Figure 1. Outline of tadpole of *Rana clamitans*. Individuals used for regeneration from old tissue have the original removal level at B and the second level at A. Individuals used for regeneration from new tissue have the original removal level at A and the second level at B. Regenerations from the second levels are compared.

The data are given in Table 1. The removed tail lengths are the lengths of the original removed portions of the tail plus or minus the

EXPLANATION OF TABLE I.

Note 1. The removed length is the length of the original removed portion of the tail plus or minus the distance of the new cut surface from the dividing line between the old and new tissue.

Note 2. The lengths as given are the living lengths. Measurements were made on material killed in Gilson's mercuro-nitric mixture and preserved in 85% alcohol. Sets I and IX were measured both when alive and after killing and preserving. From them the shrinkage coefficient was obtained and this made possible the reduction of all the data to the living basis.

Note 3. The specific amount regenerated in any case is the amount regenerated per unit of removed length.

Note 4. The average includes only the sets in which both individuals are present.

TABLE I.

Series 3628-3675

Set	Old or New tissue at cut surface	Catalog number	Total length mm.	Tail length mm.	Removed length mm.	Regeneration Time 6 days		Regeneration Time 8 days	
						Regenerated length mm.	Specific length regenerated	Regenerated length mm	Specific length regenerated
I	old	3628	38.0	24.1	13.2	2.2	0.17	3.5	0.27
	new	3629	39.2	24.6	12.8	2.3	0.18	3.1	0.24
II	old	3633	35.7	23.2	12.3	2.0	0.16	3.4	0.28
	new	3632	33.8	22.1	10.2	1.8	0.18	—	—
III	old	3636	35.8	23.1	12.8	2.0	0.16	3.25	0.25
	new	3637	38.4	25.0	11.9	2.4	0.20	3.5	0.29
IV	old	3641	32.9	20.8	11.3	1.7	0.15	3.4	0.30
	new	3640	31.4	20.4	9.3	2.2	0.24	—	—
V	old	3645	37.5	23.8	11.5	2.2	0.19	—	—
	new	3644	42.8	29.2	15.1	2.3	0.15	—	—
VI	old	3649	37.0	25.6	11.2	2.3	0.21	3.1	0.28
	new	3648	35.9	23.3	9.9	2.1	0.21	3.1	0.31
VII	old	3652	31.3	20.8	—	—	—	—	—
	new	3653	29.0	19.2	9.2	2.4	0.26	3.6	0.39
VIII	old	3656	31.8	21.1	13.2	2.4	0.18	—	—
	new	3657	33.0	22.0	11.7	2.7	0.23	4.9	0.42
IX	old	3660	26.5	17.0	9.6	2.5	0.26	3.5	0.36
	new	3661	29.4	19.0	8.7	2.0	0.23	3.0	0.34
X	old	3668	31.1	20.8	9.2	1.6	0.17	2.3	0.25
	new	3669	32.4	21.8	8.9	1.8	0.20	2.5	0.28
XI	old	3672	24.4	15.8	8.6	2.7	0.31	3.5	0.41
	new	3673	28.5	18.1	8.7	1.9	0.22	3.5	0.40
Average of old			32.9	21.5	11.3	2.16	0.196	3.19	0.303
Average of new			34.0	22.2	10.7	2.15	0.204	3.12	0.310
Old—ahead						0.01	—	0.07	—
New—ahead						—	0.008	—	0.007
Old—Times ahead						4	3½	3	3
New—Times ahead						6	6½	3	3

distances of the new cut surface from the dividing line between the old and the new tissue. The regenerated lengths as given are the living lengths. Measurements were made on material killed in Gilson's mercuro-nitric fluid and preserved in 85% alcohol. Sets I and IX were measured both when alive and after killing and preserving. From them the shrinkage coefficient was obtained and this made possible the reduction of all the data to the living basis. The averages include only the sets in which both individuals are present. The specific amount of regeneration is the amount regenerated per unit of removed length. It has been shown that within wide limits this is a constant if the only variable in the experiment is the amount removed. This statement holds for all levels in the present experiment.

The table shows that the average amount regenerated at the end of six days is 2.16 mm. from the old tissue levels and 2.15 mm. from the new tissue levels. The new tissue levels however represent the shorter amount removed, 10.7 mm. as opposed to 11.3 for the old tissue levels. This gives an average specific rate of 0.204 for the new levels and 0.196 for the old levels. The difference is probably not significant. The individual specific amounts in pairs, putting the old tissue first and the new tissue second in each case, are 0.17 and 0.18, 0.16 and 0.18, 0.16 and 0.20, 0.15 and 0.24, 0.19 and 0.15, 0.21 and 0.21, 0.18 and 0.23, 0.26 and 0.23, 0.17 and 0.20, and 0.31 and 0.22. The old tissue is ahead three times, the new six times and there is a tie in one case.

At the end of eight days the result is similar. There is a slight advantage in favor of the new tissue level but this cannot be considered as significant. The average amount regenerated is 3.19 mm. from old tissue levels and 3.12 mm. from new tissue levels. The specific amount regenerated is 0.303 for the old and 0.310 for the new level. The individual amounts by pairs putting the old tissue level first as before are 0.27 and 0.24, 0.25 and 0.29, 0.28 and 0.31, 0.36 and 0.34, 0.25 and 0.28, and 0.41 and 0.40. Each level is ahead of the other in three of the six cases.

Experiment II Series 3676-3765

Tadpoles of *Rana clamitans* with an average length of forty mm. were used. The experiment was designed for a study of the effect of successive removal on the rate of regeneration but incidentally furnishes valuable data for the present problem. In removing the regenerated portion, the cut in most cases did not come exactly at the border. In some cases it was too near the base of the tail and therefore the cells at the cut surface were old unregenerated cells. In other cases it was too near the tip of the tail and the cells at the cut surface were newly regenerated ones.

The operations were at different levels in different individuals but the determination of the specific amounts of regeneration according to the method given in the explanation of Experiment I eliminates these differences within wide limits. It does not hold when the level of the cut is very near the tip or near the base of the tail. In the present experiment the specific amount is a fair constant for all removed lengths of over 4 mm. The individuals with a removed length of less than 4 mm. are therefore treated separately. Likewise it does not hold for the first few days of regeneration during which regeneration is confined to active migration of cells over the cut surface without any new formation by cell division. Separate comparisons are made at 4, 6, 8, 10, 12½, 18 and 56 days of regeneration. The data are given in Tables 2 to 17.

Taking first the cases with a removed length of over 4 mm. there is at four days a specific amount of 0.043 for old tissue and of 0.045 for new tissue. At six days the amounts are respectively 0.135 and 0.143, at eight days 0.216 and 0.224, at ten days 0.292 and 0.293, at twelve and a half days 0.331 and 0.337, at eighteen days 0.352 and 0.348, and at fifty-six days 0.345 and 0.346. The two are approximately equal though in six out of the seven cases the new tissue is ahead. The average difference in favor of the new tissue is 0.003.

For removed amounts of less than 4 mm. the data are unsatisfactory because there are only three individuals with regeneration from new tissues. The data are however of value in comparison with the others. The specific amounts at the different days, again putting the old tissue first in each case, are 0.119 and 0.160 for four days, 0.317 and 0.327 for six days, 0.444 and 0.467 for eight days, 0.506 and 0.520 for ten days, 0.517 and 0.517 for twelve and a half days, 0.501 and 0.507 for eighteen days, and 0.475 and 0.325 for fifty-six days. In the last the absorption of the tail had begun before the measurement was made and the comparison is therefore not valid for our purposes. In the first, 0.119 for old and 0.160 for new at four days, the great difference between individual cases on each side makes a comparison of doubtful validity. There are other data however which make it probable that the initial migration of the cells takes place more rapidly from new than from old tissue. For the other levels there is on the average a slight difference (0.011) in favor of the regeneration from new tissue. With but a single exception, which is a tie, the new tissue is ahead of the old. The differences favoring the new tissue are greater than those for the larger removals. This again may be due to the fact that a larger percentage of the regenerated material is derived from the old by migration and a smaller percentage by cell division. The data unfortunately are based on such a small number of individuals, especially in the case of new tissue levels, that too much stress should not be laid on the differences.

TABLE 2

Series 3676-3765 Over 4 millimeters removed Regeneration: 4 days

Old tissue				New tissue			
Catalog number	Length removed mm.	Length regenerated mm.	Specific length regenerated	Catalog number	Length removed mm.	Length regenerated mm.	Specific length regenerated
3720	4.7	0.42	0.09	3756	4.8	0.36	0.07
3684	5.5	0.15	0.03	3751	6.7	0.45	0.07
3715	7.9	0.24	0.03	3697	7.3	0.48	0.07
3757	8.0	0.42	0.05	3721	8.5	0.57	0.07
3694	8.7	0.45	0.05	3733	8.5	0.36	0.04
3685	9.3	0.60	0.06	3734	8.5	0.48	0.06
3686	14.5	0.60	0.04	3739	9.4	0.36	0.04
3753	16.8	0.42	0.03	3722	12.5	0.60	0.05
3723	18.4	0.30	0.02	3716	12.7	0.39	0.03
3699	21.0	0.54	0.03	3698	12.9	0.50	0.04
				3759	15.5	0.30	0.02
				3705	17.6	0.72	0.04
				3717	17.6	0.42	0.02
				3687	19.7	0.54	0.03
Average			0.043	Average			0.045

Note 1. No. 3734 is left out in making up the averages because its specific amount from six days of regeneration on is very much in excess of that of any of the others. A probable explanation is that the end of the tail in this individual had been removed and regeneration had just started when the present operations were begun. If this is true it belongs to a longer removed length than indicated and the specific rate is wrong. Besides a highly exceptional individual even if not explained should be left out in determining the average value.

TABLE 3

Series 3676-3765 Over 4 millimeters removed Regeneration: 6 days

Old tissue				New tissue			
Catalog number	Length removed mm.	Length regenerated mm.	Specific length regenerated	Catalog number	Length removed mm.	Length regenerated mm.	Specific length regenerated
3720	4.7	0.84	0.18	3756	4.8	1.0	0.21
3648	5.5	0.7	0.13	3751	6.7	1.1	0.16
3715	7.9	0.9	0.11	3697	7.3	1.2	0.16
3757	8.0	1.2	0.15	3721	8.5	1.3	0.15
3694	8.7	1.5	0.17	3733	8.5	1.0	0.12
3685	9.3	1.2	0.13	3734	8.5	2.1	0.25
3686	14.5	2.1	0.14	3739	9.4	1.0	0.11
3753	16.8	2.0	0.12	3722	12.5	1.6	0.13
3723	18.4	2.3	0.12	3716	12.7	1.7	0.13
3699	21.0	2.2	0.10	3698	12.9	1.5	0.12
				3759	15.5	2.0	0.13
				3705	17.6	2.0	0.11
				3717	17.6	2.6	0.15
				3687	19.7	2.6	0.18
Average			**0.135**	**Average**			**0.143**

TABLE 4

Series 3676-3765 Over 4 millimeters removed Regeneration: 8 days

Old tissue				New tissue			
Catalog number	Length removed mm.	Length regenerated mm.	Specific length regenerated	Catalog number	Length removed mm.	Length regenerated mm.	Specific length regenerated
3720	4.7	1.1	0.23	3756	4.8	1.3	0.27
3684	5.5	1.2	0.22	3751	6.7	1.7	0.25
3715	7.9	1.7	0.22	3697	7.3	1.7	0.23
3757	8.0	2.1	0.26	3721	8.5	1.9	0.22
3694	8.7	2.2	0.25	3733	8.5	1.9	0.22
3685	9.3	1.9	0.20	3734	8.5	3.1	0.36
3686	14.5	3.4	0.23	3739	9.4	1.8	0.19
3753	16.8	2.5	0.15	3722	12.5	2.6	0.21
3723	18.4	3.7	0.20	3716	12.7	2.4	0.19
3699	21.0	4.3	0.20	3698	12.9	3.3	0.26
				3759	15.5	3.0	0.19
				3705	17.6	3.6	0.20
				3717	17.6	3.6	0.20
				3687	19.7	5.6	0.28
Average			**0.216**	**Average**			**0.224**

TABLE 5

Series 3676-3765 Over 4 millimeters removed Regeneration: 10 days

Old tissue				New tissue			
Catalog number	Length removed mm.	Length regenerated mm.	Specific length regenerated	Catalog number	Length removed mm.	Length regenerated mm.	Specific length regenerated
3720	4.7	1.3	0.28	3756	4.8	1.7	0.35
3684	5.5	1.4	0.25	3751	6.7	2.1	0.31
3715	7.9	2.3	0.29	3697	7.3	2.2	0.30
3757	8.0	2.8	0.35	3721	8.5	2.3	0.27
3694	8.7	3.2	0.37	3733	8.5	2.4	0.28
3685	9.3	2.3	0.25	3734	8.5	4.5	0.53
3686	14.5	4.8	0.33	3739	9.4	2.4	0.26
3753	16.8	3.8	0.23	3722	12.5	3.6	0.29
3723	18.4	5.3	0.29	3716	12.7	3.4	0.27
3699	21.0	5.9	0.28	3698	12.9	4.3	0.33
				3759	15.5	4.2	0.27
				3705	17.6	4.8	0.28
				3717	17.6	5.2	0.30
				3687	19.7	6.0	0.30
Average			0.292	Average			0.293

TABLE 6

Series 3676-3765 Over 4 millimeters removed Regeneration: 12-13 days

Old tissue				New tissue			
Catalog number	Length removed mm.	Length regenerated mm.	Specific length regenerated	Catalog number	Length removed mm.	Length regenerated mm.	Specific length regenerated
3720	4.7	1.3	0.28	3756	4.8	1.8	0.37
3684	5.5	1.4	0.25	3751	6.7	2.4	0.36
3715	7.9	2.6	0.33	3697	7.3	2.4	0.33
3757	8.0	3.1	0.39	3721	8.5	2.6	0.31
3694	8.7	3.4	0.39	3733	8.5	2.6	0.31
3685	9.3	2.8	0.30	3734	8.5	5.7	0.67
3686	14.5	5.3	0.37	3739	9.4	3.0	0.32
3753	16.8	5.2	0.31	3722	12.5	3.9	0.31
3723	18.4	6.5	0.35	3716	12.7	4.2	0.33
3699	21.0	7.1	0.34	3698	12.9	5.0	0.39
				3759	15.5	4.8	0.31
				3705	17.6	6.4	0.36
				3717	17.6	6.0	0.34
				3687	19.7	6.6	0.34
Average			0.331	Average			0.337

TABLE 7

Series 3676-3765 Over 4 millimeters removed Regeneration: 17-18-19 days

Old tissue				New tissue			
Catalog number	Length removed mm.	Length regenerated mm.	Specific length regenerated	Catalog number	Length removed mm.	Length regenerated mm.	Specific length regenerated
3720	4.7	1.3	0.28	3756	4.8	1.6	0.33
3684	5.5	1.5	0.27	3751	6.7	2.5	0.37
3715	7.9	2.6	0.33	3697	7.3	2.3	0.32
3757	8.0	3.2	0.40	3721	8.5	2.3	0.27
3694	8.7	3.4	0.39	3733	8.5	2.6	0.31
3685	9.3	3.0	0.32	3734	8.5	6.4	0.75
3686	14.5	5.2	0.36	3739	9.4	2.9	0.31
3753	16.8	6.4	0.38	3722	12.5	3.5	0.28
3723	18.4	8.1	0.43	3716	12.7	5.1	0.40
3699	21.0	7.5	0.36	3698	12.9	5.4	0.42
				3759	15.5	6.7	0.43
				3705	17.6	6.2	0.35
				3717	17.6	6.7	0.38
				3687	19.7	7.0	0.36
Average			0.352	Average			0.348

TABLE 8

Series 3676-3765 Over 4 millimeters removed Regeneration: 55-56-57 days

Old tissue				New tissue			
Catalog number	Length removed mm.	Length regenerated mm.	Specific length regenerated	Catalog number	Length removed mm.	Length regenerated mm.	Specific length regenerated
3720	4.7	1.3	0.28	3756	4.8	—	——
3684	5.5	1.4	0.25	3751	6.7	2.3	0.34
3715	7.9	2.8	0.35	3697	7.3	2.1	0.29
3757	8.0	3.1	0.39	3721	8.5	2.2	0.26
3694	8.7	—	——	3733	8.5	2.8	0.33
3685	9.3	2.6	0.28	3734	8.5	6.6	0.78
3686	14.5	—	——	3739	9.4	—	——
3753	16.8	7.1	0.42	3722	12.5	4.2	0.34
3723	18.4	8.3	0.45	3716	12.7	4.4	0.35
3699	21.0	7.2	0.34	3698	12.9	5.4	0.42
				3759	15.5	6.6	0.43
				3705	17.6	6.0	0.34
				3717	17.6	6.4	0.36
				3687	19.7	—	——
Average			0.345	Average			0.346

TABLE 9

Series 3676-3765 Over 4 millimeters removed Summary Tables 2 to 8

Table number	Days of regeneration	Old tissue Specific length of regeneration	New tissue Specific length of regeneration	Old ahead	New ahead
2	4	0.043	0.045		0.002
3	6	0.135	0.143		0.008
4	8	0.216	0.224		0.008
5	10	0.292	0.293		0.001
6	12, 13	0.331	0.337		0.006
7	17, 18, 19	0.352	0.348	0.004	
8	55, 56, 57	0.345	0.346		0.001
Average					0.003

TABLE 10

Series 3676-3765 Less than 4 millimeters removed Regeneration: 4 days

Old tissue				New tissue			
Catalog number	Length removed mm.	Length regenerated mm.	Specific length regenerated	Catalog number	Length removed mm.	Length regenerated mm.	Specific length regenerated
3676	1.3	0.27	0.27	3696	2.1	0.48	0.23
3682	1.6	0.18	0.11	3749	2.8	0.30	0.11
3730	1.6	0.39	0.24	3750	3.5	0.48	0.14
3754	1.6	0.06	0.04				
3718	2.1	0.06	0.03				
3731	2.7	0.15	0.06				
3713	2.8	0.36	0.13				
3719	3.1	0.36	0.12				
3701	3.2	0.42	0.13				
Average			0.119	Average			0.160

TABLE 11

Series 3676-3765 Less than 4 millimeters removed Regeneration: 6 days

Old tissue				New tissue			
Catalog number	Length removed mm.	Length regenerated mm.	Specific length regenerated	Catalog number	Length removed mm.	Length regenerated mm.	Specific length regenerated
3676	1.3	0.6	0.46	3696	2.1	0.85	0.40
3682	1.6	0.6	0.37	3749	2.8	0.6	0.21
3730	1.6	0.75	0.47	3750	3.5	1.3	0.37
3754	1.6	0.55	0.34				
3718	2.1	0.45	0.21				
3731	2.7	0.5	0.19				
3713	2.8	0.8	0.29				
3719	3.1	0.84	0.27				
3701	3.2	0.8	0.25				
Average			0.317	Average			0.327

TABLE 12

Series 3676-3765 Less than 4 millimeters removed Regeneration: 8 days

Old tissue				New tissue			
Catalog number	Length removed mm.	Length regenerated mm.	Specific length regenerated	Catalog number	Length removed mm.	Length regenerated mm.	Specific length regenerated
3676	1.3	0.9	0.69	3696	2.1	1.0	0.48
3682	1.6	0.9	0.56	3749	2.8	1.2	0.43
3730	1.6	0.9	0.56	3750	3.5	1.7	0.49
3754	1.6	0.9	0.56				
3718	2.1	0.7	0.33				
3731	2.7	0.8	0.29				
3713	2.8	0.9	0.32				
3719	3.1	1.1	0.35				
3701	3.2	1.1	0.34				
Average			0.444	Average			0.467

TABLE 13

Series 3676-3765 Less than 4 millimeters removed Regeneration: 10 days

Old tissue				New tissue			
Catalog number	Length removed mm.	Length regenerated mm.	Specific length regenerated	Catalog number	Length removed mm.	Length regenerated mm.	Specific length regenerated
3676	1.3	0.9	0.69	3696	2.1	1.1	0.52
3682	1.6	1.0	0.62	3749	2.8	1.4	0.50
3730	1.6	0.9	0.56	3750	3.5	1.9	0.54
3754	1.6	1.1	0.69				
3718	2.1	1.0	0.48				
3731	2.7	1.0	0.37				
3713	2.8	0.9	0.32				
3719	3.1	1.4	0.45				
3701	3.2	1.2	0.37				
Average			**0.506**	**Average**			**0.520**

TABLE 14

Series 3676-3765 Less than 4 millimeters removed Regeneration: 12-13 days

Old tissue				New tissue			
Catalog number	Length removed mm.	Length regenerated mm.	Specific length regenerated	Catalog number	Length removed mm.	Length regenerated mm.	Specific length regenerated
3676	1.3	0.9	0.69	3696	2.1	1.0	0.48
3682	1.6	1.0	0.62	3749	2.8	1.4	0.50
3730	1.6	0.9	0.56	3750	3.5	2.0	0.57
3754	1.6	1.2	0.75				
3718	2.1	1.0	0.48				
3731	2.7	1.0	0.37				
3713	2.8	0.9	0.32				
3719	3.1	1.4	0.45				
3701	3.2	1.3	0.41				
Average			**0.517**	**Average**			**0.517**

TABLE 15

Series 3676-3765   Less than 4 millimeters removed   Regeneration: 17-18-19 days

Old tissue				New tissue			
Catalog number	Length removed mm.	Length regenerated mm.	Specific length regenerated	Catalog number	Length removed mm.	Length regenerated mm.	Specific length regenerated
3676	1.3	0.9	0.69	3696	2.1	1.0	0.48
3682	1.6	1.0	0.62	3749	2.8	1.3	0.47
3730	1.6	0.9	0.56	3750	3.5	2.0	0.57
3754	1.6	1.2	0.75				
3718	2.1	0.5	0.24				
3731	2.7	—	——				
3713	2.8	0.9	0.32				
3719	3.1	1.3	0.42				
3701	3.2	1.3	0.41				
Average			0.501	Average			0.507

TABLE 16

Series 3676-3765   Less than 4 millimeters removed   Regeneration: 55-56-57 days

Old tissue				New tissue			
Catalog number	Length removed mm.	Length regenerated mm.	Specific length regenerated	Catalog number	Length removed mm.	Length regenerated mm.	Specific length regenerated
3676	1.3	0.7	0.54	3696	2.1	0.7	0.33
3682	1.6	1.1	0.69	3749	2.8	0.9	0.32
3730	1.6	0.7	0.44	3750	3.5	—	——
3754	1.6	1.1	0.69				
3718	2.1	—	——				
3731	2.7	—	——				
3713	2.8	0.5	0.18				
3719	3.1	—	——				
3701	3.2	1.0	0.31				
Average			0.475	Average			0.325

TABLE 17

Series 3676-3765 Less than 4 millimeters removed Summary Tables 10 to 16

Table number	Days of regeneration	Old tissue Specific length of regeneration	New tissue Specific length of regeneration	Old ahead	New ahead
10	4	0.119	0.160		0.041
11	6	0.317	0.327		0.010
12	8	0.444	0.467		0.023
13	10	0.506	0.520		0.014
14	12, 13	0.517	0.517	0.000	0.000
15	17, 18, 19	0.501	0.507		0.006
16	55, 56, 57	0.475	0.325	0.150	
Average					0.011

Note 1. Because of the great variability in the data the average for the four-day period is not of much value and is therefore not included in the grand average.

Note 2. The absorption of the regenerated portion of the tail was proceeding so rapidly by the fifty-fifth day of regeneration that this average should not be included in the grand average.

EXPERIMENT III SERIES 3557-3624

This experiment was planned for a study of the effect of repeated removal and regeneration upon the rate of metamorphosis but it yields data of value for the present problem. Tadpoles of *Rana clamitans* with an average length of about 40 mm. were used. In some cases the cuts were made inside of the first level and therefore in old tissue and in other cases outside of the first level and therefore in new tissue.

The data include third, fourth and fifth successive regenerations. The time of regeneration is 37 days for the third and 36 days for the fourth and for the fifth regenerations. The length of time is more than sufficient for the completion of the process of regeneration in so far as it is completed. The data therefore do not serve for the rate but for the completeness of regeneration from old as compared with new levels. Approximately one-half of the original tail length was removed but measurements were not made of individual removed lengths, so that specific rates of regeneration can not be calculated. However the removed lengths were so nearly alike as to make the regenerated lengths of value in direct comparison.

The data are given in Table 18. The average length of the third regeneration is 7.9 mm. for both the old and the new tissue basis. For the fourth regeneration the value from old tissue is 5.3 mm. and from new tissue 5.5 mm. The corresponding values for the fifth regeneration are 6.6 mm. and 5.9 mm. Averaging the individual cases for all three regenerations the old tissue average is 6.5 mm. and the new tissue average 6.6 mm., an advantage in favor of the latter of 0.1 mm. This difference can not be considered as significant, especially since for the individual regenerations the two levels give equal regenerated lengths for the third, the new is slightly ahead at the fourth and the old is ahead at the fifth.

On the whole the data for Experiment III agree with those for Experiments I and II. There is no striking difference between completeness of regeneration from old and from new tissue levels, though a small difference favoring the latter persists in practically all the comparisons.

TABLE 18

Rana clamitans Series 3557-3624

Regenerated tail length from new tissue compared with that from old tissue during the third, fourth and fifth regenerations

	Third regeneration		Fourth regeneration		Fifth regeneration		Third, fourth and fifth regenerations combined	
	37 Days		36 Days		36 Days			
	Old tissue	New tissue	Old tissue	New tissue	Old tissue	New tissue	Old tissue	New tissue
	2.0	5.7	4.4	4.9	4.7	5.2		
	6.8	6.6	4.5	5.4	5.5	5.7		
	6.9	8.0	4.8	5.5	6.2	5.9		
	7.5	8.3	4.9	6.1	6.5	6.8		
	7.9	9.3	5.0		7.1			
	9.0	9.7	5.1		7.2			
	9.4		5.8		7.9			
			6.1		8.0			
			7.3					
Average in mm.	7.9	7.9	5.3	5.5	6.6	5.9	6.5	6.6
Difference in mm.	0.0	0.0		+0.2	+0.7			+0.1

DISCUSSION

While the knowledge of the relative rates of regeneration for old and new tissue is essential for accurate determination of other factors its main interest is in its bearing on the question of the character of control of the process of regeneration. Evidence from a great many directions points toward the conclusion that regeneration is not wholly a direct response of the injured cells at the cut surface nor of those in the immediate neighborhood of the cut surface. It is more and more evident that conditions in parts of the body remote from the injured region are involved. If rate of regeneration were determined wholly by the character of the cells at the cut surface we would expect that cells in process of active proliferation, such as those that are starting to build up a new tail, would respond much more promptly than those which have become more highly differentiated and hence more stable. Regenerating cells ought to furnish a much better basis than old ones. We find however that there is no striking difference in the two cases. Regeneration proceeds at approximately the same rate whether old or new cells have furnished the basis for the new material. It is true that the data show on the average a slight advantage in favor of the new tissue, especially during the early periods, but this advantage is small and it is doubtful whether it can be considered as significant. There is some evidence that the earliest stages of regeneration, those due to cell migration exclusively, are more rapid from new than from old tissue. If this evidence is reliable an explanation is found for the slight advantage in favor of the new tissue at later periods.

SUMMARY

1. A comparison of the rate of regeneration in tadpoles of *Rana clamitans* in cases where there are newly regenerated cells at the cut surface with those in which only old cells are present shows, on the whole, little difference between the two.

2. The slight difference favors the new cells but may not be significant.

3. In Experiment I the specific length of regeneration at the end of 6 days was 0.196 from old tissue and 0.204 from new tissue.

4. In the same experiment at the end of 8 days the specific length from the old was 0.303 and from the new 0.310.

5. In Experiment II the general result was similar to that in Experiment I. The amounts of regeneration in the two cases are very nearly equal and the slight difference is in favor of the new tissue.

6. Experiment III shows that as regards completeness of regen-

eration there is again essential similarity between the old tissue and the new tissue levels.

7. The result strengthens the view that the rate of regeneration is controlled in large part by factors not inherent in the character or condition of the cells near the cut surface.

8. In the case of the earliest stages, those in which there is cell migration but no cell division, there is some evidence that the rate of regeneration may be greater from new than from old tissue.

PART II

THE EFFECT OF SUCCESSIVE REMOVAL UPON THE RATE AND COMPLETENESS OF REGENERATION

One of the most interesting facts in connection with regeneration is the ability to replace a part after repeated removal. The present set of experiments was made in continuation of previous studies of the effect of successive removal upon the rate of regeneration (Zeleny 1907, 1908, 1909). The earlier studies show that as a rule the rate of regeneration following a first removal is no greater than that following second and later removals if the effect of age is eliminated. Where a difference exists it seems to be in favor of the later regenerations.

The matter is of very great interest in connection with general problems of development and particularly in connection with the question as to the existence or non-existence of a necessary limit to the amount of living substance that a single individual may produce during its life cycle. Does the production of a group of tissues use up a part of a certain store of developmental energy or of developmental factors possessed by the individual or is this store inexhaustible or perchance even increased by exercise of the function? These questions warrant more extended study especially in view of the additional analysis that has been made of other factors controlling the rate of regeneration. The paper includes all the unpublished data that have been obtained on the problem at hand. In general these data support the conclusions previously reached. The descriptions of the individual experiments will first be given and they will be followed by a discussion of the general results.

EXPERIMENT I RANA CLAMITANS SERIES 3628-3675

Material and Method The tadpoles were collected on December 9, 1911. At the time of the operation on December 20 the average total length was 33.0 mm. and the average tail length 21.6 mm. Forty-eight individuals were divided into twelve sets of four each. The four individuals of a set are called *a*, *b*, *c*, and *d*. Approximately one-half in length of the tail was removed by a transverse cut in *c* and *d*. After 21 days the regenerated portion of the tail was removed. In individual *c* the second cut came inside of the border line between old and new tissue and in individual *d* it came outside of that line. Of the two individuals available for second regeneration in each set, the one with the cut nearer to the tip of the tail was chosen as individual *c* and the other as individual *d*. In this way the second regeneration levels were equalized. A first removal of a half of the tail was made in individuals *a* and *b* at the same time that the second removal was made in *c* and *d*. A direct comparison of the rate of the second regeneration with that of the first was thus made possible without the complication due to internal factors such as difference in age, or external factors such as temperature and food.

Measurements of regenerated lengths were made at the end of six and of eight days, other experiments having shown that the period of most rapid growth comes at about this time.

Elsewhere there is a comparison of the rate of regeneration from new tissue with that from old tissue. Here the chief concern is the comparison of the rate of the second regenerations, including both old tissue and new tissue levels, with first regenerations.

Data The results of the experiment are given in Table 19 for six-day regenerations and in Table 20 for eight-day regenerations. At the end of six days the average length of first regenerations is 2.01 mm. and of second regenerations 2.18 mm. The first exceeds the second in two cases, the second exceeds the first in eight and one is tied. The corresponding average specific amounts are 0.194 and 0.205. In five cases the first exceeds the second and in six the second exceeds the first.

At eight days the average length of the first regenerations is 3.06 mm. and of the second 3.42 mm. The first exceeds the second in three sets and the second exceeds the first in seven sets. The corresponding average specific amounts are 0.298 and 0.323. In four the first exceeds the second regeneration and in six the second exceeds the first.

Comparing the first regenerations on the one hand with second regenerations from old tissue and on the other hand with second regenerations from new tissue it is found, including only complete sets, that at the end of six days the average first regeneration length is 2.01 mm. while that of the second from new tissue is 2.15 mm. and from old tissue 2.16 mm. The corresponding average specific amounts are 0.194 for first regenerations and 0.196 for second regenerations from old tissue and 0.204 for second regenerations from new tissue.

At eight days the first regeneration lengths average 3.06 mm. while second regenerations from old tissue average 3.19 and those from new tissue 3.12. The corresponding specific lengths are 0.298 for first regenerations and 0.303 for second from old tissue and 0.310 for second from new tissue.

TABLE 19
Rana clamitans Series 3676-3765
Comparison of first and second regenerations Age factor eliminated
Six Days

Series	Regeneration		Total length	Tail length	Length removed	Length regenerated	Specific length regenerated	Average length regenerated	Average specific length regenerated
I	1	individual a	35.5	23.1	11.5	1.9	0.17		
		individual b	34.5	21.9	9.4	1.8	0.19	1.85	0.180
	2	c from old tissue	38.0	24.1	13.2	2.2	0.17		
		d from new tissue	39.2	24.6	12.8	2.3	0.18	2.25	0.175
II	1	a	34.5	23.0	—	—	—		
		b	33.9	22.2	9.6	1.7	0.18	1.70	0.180
	2	c old	35.7	23.2	12.3	2.0	0.16		
		d new	33.8	22.1	10.2	1.8	0.18	1.90	0.170
III	1	a	36.2	23.3	9.7	1.7	0.18		
		b	34.1	22.5	10.9	1.9	0.17	1.80	0.175
	2	c old	35.8	23.1	12.8	2.0	0.16		
		d new	38.4	25.0	11.9	2.4	0.20	2.20	0.180
IV	1	a	33.1	21.2	12.6	2.2	0.17		
		b	32.4	20.8	10.2	1.7	0.17	1.95	0.170
	2	c old	32.9	20.8	11.3	1.7	0.15		
		d new	31.4	20.4	9.3	2.2	0.24	1.95	0.195
V	1	a	40.8	27.3	11.9	2.1	0.18		
		b	39.4	26.4	12.7	2.2	0.17	2.15	0.175
	2	c old	37.5	23.8	11.5	2.2	0.19		
		d new	42.8	29.2	15.1	2.3	0.15	2.25	0.170
VI	1	a	37.0	24.5	10.2	1.9	0.19		
		b	35.7	24.6	12.9	2.2	0.17	2.05	0.180
	2	c old	37.0	25.6	11.2	2.3	0.21		
		d new	35.9	23.3	9.9	2.1	0.21	2.20	0.210
VII	1	a	31.2	20.1	11.9	2.1	0.18		
		b	28.0	18.6	8.4	2.0	0.24	2.05	0.210
	2	c old	31.3	20.8	—	—	—		
		d new	29.0	19.2	9.2	2.4	0.26	2.40	0.260

TABLE 19 (Continued)

Series	Regeneration		Total length	Tail length	Length removed	Length regenerated	Specific length regenerated	Average length regenerated	Average specific length regenerated
VIII	1	a	28.7	18.5	10.0	2.1	0.21		
		b	32.0	21.5	8.5	2.2	0.26	2.17	0.235
	2	c old	31.8	21.1	13.2	2.4	0.18		
		d new	33.0	22.0	11.7	2.7	0.23	2.55	0.205
IX	1	a	29.8	19.1	10.1	2.3	0.23		
		b	26.9	17.0	10.7	2.3	0.22	2.30	0.225
	2	c old	26.5	17.0	9.6	2.5	0.26		
		d new	29.4	19.0	8.7	2.0	0.23	2.25	0.245
X	1	a	32.1	21.5	12.0	2.3	0.19		
		b	32.4	21.5	10.1	2.0	0.20	2.15	0.195
	2	c old	32.7	22.4	—	—	—		
		d new	30.0	19.8	—	—	—	—	—
XI	1	a	30.9	20.9	10.2	2.0	0.20		
		b	30.1	20.2	9.4	1.8	0.20	1.90	0.200
	2	c old	31.1	20.8	9.2	1.6	0.17		
		d new	32.4	21.8	8.9	1.8	0.20	1.70	0.185
XII	1	a	28.0	18.0	11.0	2.2	0.20		
		b	26.3	16.4	10.4	2.1	0.20	2.15	0.200
	2	c old	24.4	15.4	8.6	2.7	0.31		
		d new	28.5	18.1	8.7	1.9	0.22	2.30	0.265
Average	**1**		**32.7**	**21.4**	**10.6**			**2.01**	**0.194**
	2		**33.4**	**21.8**	**10.9**			**2.18**	**0.205**

The data as a whole show an advantage in favor of the second regeneration as compared with the first. This is seen not only when the direct regenerated lengths are taken but also when the specific amounts are used. Elsewhere it is shown that the specific amount of regeneration is independent of the level of the cut and therefore a constant within the limits of removal as used in this experiment. The specific amount determinations are therefore more accurate for our purposes than the direct values of length regenerated.

The first regeneration is slightly below the second not only in case the latter is from new cells but also in case it is from old cells. The difference between first and second regenerations therefore can not be due entirely to the presence in the former of cells which are already undergoing regeneration.

TABLE 20

Rana clamitans Series 3628-3675

First and second regenerations compared Age factor eliminated

Eight days

Series	Regeneration		Length removed	Length regenerated	Specific length regenerated	Average length regenerated	Average specific length regenerated
I	1	individual a	11.5	3.1	0.26		
		individual b	9.4	2.5	0.27	0.28	0.265
	2	c from old tissue	13.2	3.5	0.27		
		d from new tissue	12.8	3.1	0.24	3.30	0.255
II	1	a	—	—	—		
		b	9.6	2.1	0.22	2.10	0.220
	2	c old	12.3	3.4	0.28		
		d new	10.2	—	—	3.40	0.280
III	1	a	9.7	2.7	0.28		
		b	10.9	3.4	0.31	3.05	0.295
	2	c old	12.8	3.25	0.25		
		d new	11.9	3.5	0.29	3.37	0.270
IV	1	a	12.6	3.25	0.26		
		b	10.2	3.25	0.32	3.25	0.290
	2	c old	11.3	3.4	0.30		
		d new	9.3	—	—	3.40	0.300
V	1	a	11.9	—	—		
		b	12.7	4.0	0.31	4.00	0.310
	2	c old	11.5	—	—		
		d new	15.1	—	—	—	—

TABLE 20 (Continued)

Series	Re-generation		Length removed	Length regenerated	Specific length regenerated	Average length regenerated	Average specific length regenerated
VI	1	a	10.2	3.6	0.35		
		b	12.9	3.6	0.28	3.60	0.315
	2	c old	11.2	3.1	0.28		
		d new	9.9	3.1	0.31	3.10	0.295
VII	1	a	11.9	3.8	0.32		
		b	8.4	3.25	0.39	3.52	0.355
	2	c old	—	—	—		
		d new	9.2	3.6	0.39	3.60	0.390
VIII	1	a	10.0	3.25	0.32		
		b	8.5	3.4	0.40	3.32	0.360
	2	c old	13.2	—	—		
		d new	11.7	4.9	0.42	4.90	0.420
IX	1	a	10.1	3.2	0.32		
		b	10.7	3.4	0.32	3.30	0.320
	2	c old	9.6	3.5	0.36		
		d new	8.7	3.0	0.34	3.25	0.350
X	1	a	12.1	3.6	0.30		
		b	10.1	2.3	0.23	2.95	0.265
	2	c old	—	—	—		
		d new	—	—	—	—	—
XI	1	a	10.2	3.5	0.34		
		b	9.4	2.5	0.27	3.00	0.305
	2	c old	9.2	2.3	0.25		
		d new	8.9	2.5	0.28	2.40	0.265
XII	1	a	11.0	—	—		
		b	10.4	2.7	0.26	2.70	0.260
	2	c old	8.6	3.5	0.41		
		d new	8.7	3.5	0.40	3.50	0.405
Average	1		10.6			3.06	0.298
	2		10.9			3.42	0.323

Experiment II Rana clamitans Series 3676-3765

Material and Method Ninety tadpoles with an average total length of about 40 mm. and an average tail length of 27 mm. were used in the experiment. The plan consisted in the removal of a portion of the tail in a part, S, of the individuals, the remaining part, F, being left uninjured at the time. After S had been regenerating a new tail for twenty-two days both S and F were operated upon. In S the regenerating tails were removed by a cut which came at the border line between the old and the new tissues. In F an operation was made similar to the original one on S and leaving the same amount of old tail in both S and F. The procedure is similar to that shown in Figure 1. S and F were now allowed to regenerate and a direct comparison is possible between a second regeneration in S and a first regeneration in F.

Measurements were made of regenerated lengths at 4, 6, 8, 10, 12½, 18 and 56 days. The operations were made at six levels corresponding approximately to the removal respectively of $^1/_{18}$, $^1/_{10}$, ⅙, ⅓, ½ and ⅔ of the tail. Four of these levels, $^1/_{10}$, ⅓, ½ and ⅔, had at least five individuals each for each regeneration. The other two levels, $^1/_{18}$ and ⅙, had less than five individuals per regeneration but are included in the tables though their averages are not as reliable as those of the others.

The method as described agrees in principle with that pursued in Experiment I. It has a decided advantage over a direct comparison within a single individual because it eliminates the age factor as well as the effects of change in external conditions such as temperature and food.

Data The results of the experiment are given in Tables 21 to 30 and in Figures 2 and 3. The data show on the whole a tendency for the second regeneration to remain in advance of the first for eight or ten days after the operation. The first regeneration then catches up and even slightly surpasses the other; this is apparent both when the regenerated lengths are taken directly and when they are corrected for difference in level of the cut and put in terms of specific regenerated length or the length regenerated per unit of removed length.

In making the comparisons certain general features must be borne in mind. The maximum rate of regeneration is reached on or near the seventh day, earlier for the smaller removals and later for the larger removals. The whole regeneration, in so far as it is completed, is finished in nearly all cases at 12½ days, again somewhat earlier for the smaller and somewhat later for the larger removals. In the tadpoles used in the present experiment about four-tenths in length of the removed tail is replaced before regeneration stops. This was found to be generally true of tadpoles of this size in *Rana clamitans.* The percent regenerated is somewhat greater for the smallest removals than for the others. After the maximum is reached there is a tendency toward decrease of the regenerated region though this is hard to determine with accuracy because the boundary between old and new tissue becomes more and more obscure as time goes on. For this reason the data for 56 days of regeneration are not as reliable as the others.

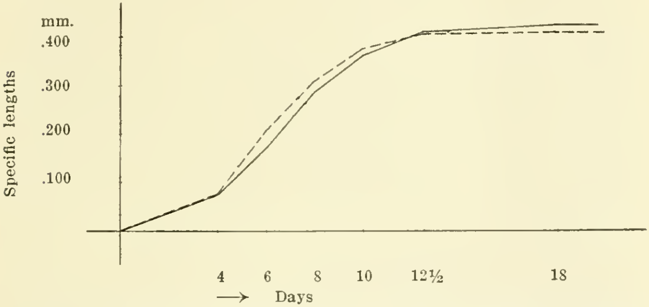

Figure 2. Specific regenerated lengths during the regenerative period for both first and second regenerations. Tadpole tail of *Rana clamitans.* Series 3676-3765.

Broken line = second regeneration.
Unbroken line = first regeneration.

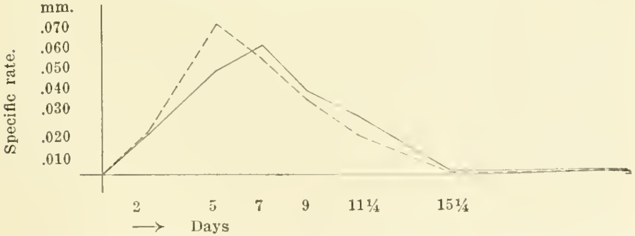

Figure 3. Change in specific rate of regeneration during the regenerative period for both first and second regenerations. Tadpole tail of *Rana clamitans.* Series 3676-3765.

Unbroken line = first regeneration.
Broken line = second regeneration.

At the four-day period the amount of regeneration is so small that there is a large probable error and these data should be used with caution. For the $^1/_{18}$ and $\frac{1}{6}$ removals the number of individuals is so small that the data for these levels do not compare in accuracy with the others and they will therefore be passed over for the present.

The data are presented in Tables 21 to 30. Tables 21 to 26 give respectively the regenerations for the six different levels beginning with the shortest removal. Table 27 collects all the data of amounts regenerated and Table 28 all the data of specific amounts regenerated. Figure 2 gives in graphic form the specific amounts regenerated for each regeneration. Table 29 gives the differences between the first and second regenerations for each of the different levels at each of the seven times of measurement. It includes the differences in specific length as well as those in absolute length. The specific lengths furnish the better basis for comparison and will be used in the following discussion unless otherwise stated. Table 30 compares the specific rates in the first and second regenerations and Figure 3 gives the results in graphic form.

Taking up the regeneration from the different levels and leaving out of consideration for the present the two levels with too small a number of individuals, the data for the $^1/_{10}$ level as given in Table 4 are the first to be considered. There are five individuals for first and seven for second regenerations. The second regeneration is ahead in specific length from the fourth to the tenth day. At 12½ days the two are tied and at 56 days the first is ahead. Regeneration is completed in 12½ days and beyond this time there is a decrease in regenerated material. The decrease is greater in the second than in the first regeneration, hence the ascendency of the latter at 56 days. During the whole period of active regeneration the second regeneration remains ahead.

There are eight individuals for the first regeneration and eleven for the second at the ⅓ level (Table 24). The specific amounts of regeneration are strikingly similar throughout the whole period of regeneration. The two departures from equality are an advantage of 0.01 for the second regeneration at 8 days and a disadvantage of 0.02 at 18 days. These departures are in the direction of the general rule observed at other levels that the second regeneration tends to be ahead at the earlier periods and the first at later periods, the advantage in the later case being due to the earlier completion of regeneration and absorption of regenerated material in the second regenerations than in the first ones. In this instance the first regeneration does not gain an advantage until after the second has reached its maximum.

At the ½ level there are 5 individuals for the first regeneration and 8 for the second (Table 25). The second is ahead until the eighth day.

Beginning with the tenth day the first is ahead. In general the advantage of the first increases as time goes on. The growth of new tissue does not terminate until the eighteenth day or after.

At the ⅔ level there are five individuals for the first and ten for the second regeneration (Table 26). The second is ahead of the first until the tenth day, after which the first is in the lead. Regeneration is not stopped until the eighteenth day or later.

At all four of these levels the specific length of the second regeneration tends to be ahead until the tenth day (Table 28 and Figure 2). The maximum rate of regeneration is reached before this time and somewhat earlier by the second than by the first regeneration, hence the relative gain by the latter after the tenth day (Table 30 and Figure 3). The stopping of regeneration also comes earlier for the second than for the first regeneration as does the beginning of absorption of regenerated material.

The data in Experiment I concern the amount of regeneration at six and at eight days. At the corresponding times in Experiment II the second regeneration is ahead of the first. There is a full agreement between the two experiments in this regard.

The more rapid rate of the second regeneration at the start may at first sight seem to be due to the presence of at least some cells which have been actively engaged in previous regenerations. If the second cut comes outside of the boundary between old and new cells the latter cover the whole new cut surface. Even if the cut seems to be exactly at the original cut level there will be some new cells at the regenerating surface. These cells which are already regenerating may be expected to adjust themselves more readily to the new conditions than old ones which have not been engaged in such a process. In another place the relative rates from old and from new tissue are described and a slight early difference favoring the new tissue is made out. While this slight initial advantage may be explained in this way it is probably confined to the period of cell migration and is not a factor in the period of cell division which begins on the second day or later. It is evident that on the whole the control of rate is not a matter inherent in the cells in the neighborhood of the cut surface. Indications point rather to a more central control of the process.

TABLE 21

Rana clamitans Series 3676-3765

Comparison of first and second regenerations Age factor eliminated

One-eighteenth of tail removed

	Catalog number	Removed length mm.	Length regenerated in mm.						
			4 Days	6 Days	8 Days	10 Days	12½ Days	18 Days	56 Days
First regeneration	3706	1.4	0.24	0.54	0.9	1.0	1.0	0.9	0.7
	3742	1.7	0.30	0.40	0.7	0.8	0.9	0.9	0.7
	Average	1.5							
Second regeneration	3676	1.3	0.27	0.60	0.9	1.0	1.0	1.0	0.7
	3682	1.6	0.18	0.60	0.9	1.0	1.0	1.0	1.1
	3730	1.6	0.39	0.75	0.9	0.9	0.9	0.9	0.7
	3754	1.6	0.06	0.55	0.9	1.1	1.2	1.2	1.1
	Average	1.5							
Av. length—First regen.			0.27	0.47	0.8	0.9	0.9	0.9	0.7
Av. length—Second regen.			0.22	0.62	0.9	1.0	1.0	1.0	0.9
Increase or decrease			—0.05	+0.15	+0.1	+0.1	+0.1	+0.1	+0.2
Specific lg.—First regen.			0.17	0.30	0.53	0.58	0.61	0.60	0.45
Specific lg.—Second regen.			0.15	0.42	0.60	0.67	0.67	0.67	0.60
Increase or decrease			—0.02	+0.12	+0.07	+0.09	+0.06	+0.07	+0.15

TABLE 22

Rana clamitans Series 3676-3765
Comparison of first and second regenerations Age factor eliminated
One-tenth of tail removed

	Catalog number	Removed length mm.	Length regenerated in mm.						
			4 Days	6 Days	8 Days	10 Days	12½ Days	18 Days	56 Days
First regeneration	3688	2.5	0.12	0.3	0.3	0.7	0.9	0.9	0.7
	3707	3.2	0.24	0.8	1.1	1.4	1.4	1.3	0.7
	3724	2.6	0.06	0.5	0.8	1.1	1.4	1.4	1.2
	3743	2.5	0.03	0.1	0.4	0.8	1.0	1.0	1.7
	3760	3.1	0.30	0.6	0.9	1.1	1.2	1.1	1.1
	Average	2.6							
Second regeneration	3677	2.0	0.30	0.6	0.9	0.9	0.9	0.9	0.7
	3696	2.1	0.48	0.8	1.0	1.1	1.0	1.0	0.7
	3713	2.8	0.36	0.8	0.9	0.9	0.9	0.9	0.5
	3719	3.1	0.36	0.8	1.1	1.4	1.4	1.3	—
	3749	2.8	0.30	0.6	1.2	1.4	1.4	1.3	0.9
	3750	3.5	0.48	1.3	1.7	1.9	2.0	2.0	—
	3701	3.2	0.42	0.8	1.1	1.2	1.3	1.3	—
	Average	2.8							
Av. length—First regen.			0.15	0.5	0.7	1.0	1.2	1.1	1.1
Av. length—Second regen.			0.39	0.8	1.1	1.3	1.3	1.2	0.8
Increase or decrease			+0.24	+0.3	+0.4	+0.3	+0.1	+0.1	—0.3
Specific lg.—First regen.			0.06	0.18	0.27	0.38	0.46	0.42	0.42
Specific lg.—Second regen.			0.14	0.30	0.39	0.46	0.46	0.43	0.29
Increase or decrease			+0.08	+0.12	+0.12	+0.08	0.00	+0.01	—0.13

TABLE 23

Rana clamitans Series 3676-3765

Comparison of first and second regeneration Age factor eliminated

One-sixth of tail removed

	Catalog number	Removed length mm.	Length regenerated in mm.						
			4 Days	6 Days	8 Days	10 Days	12½ Days	18 Days	56 Days
First regeneration	3708	5.3	0.54	1.2	1.9	2.1	2.3	2.3	1.8
	3726	4.3	0.42	0.9	1.3	1.4	1.4	1.4	1.4
	3762	4.1	0.57	1.0	1.2	1.5	1.7	1.8	1.4
	Average	4.6							
Second regeneration	3678	5.0	0.20	0.5	0.9	1.0	1.1	1.1	—
	3684	5.5	0.15	0.7	1.2	1.4	1.4	1.5	1.4
	3702	4.7	0.42	0.8	1.1	1.3	1.3	1.3	1.3
	3720	4.6	0.06	0.3	1.3	1.8	2.3	1.9	2.0
	3756	4.8	0.36	1.0	1.3	1.7	1.8	1.6	—
	Average	4.9							
Av. length—First regen.			0.51	1.0	1.5	1.7	1.8	1.8	1.5
Av. length—Second regen.			0.24	0.7	1.2	1.4	1.6	1.5	1.6
Increase or decrease			—0.27	—0.3	—0.3	—0.3	—0.2	—0.3	+0.1
Specific lg.—First regen.			0.11	0.22	0.33	0.37	0.39	0.39	0.34
Specific lg.—Second regen.			0.05	0.14	0.24	0.29	0.33	0.31	0.33
Increase or decrease			—0.06	—0.08	—0.09	—0.08	—0.06	—0.08	—0.01

TABLE 24

Rana clamitans Series 3676-3765
Comparison of first and second regenerations Age factor eliminated
One-third of tail removed

	Catalog number	Removed length mm.	Length regenerated in mm.						
			4 Days	6 Days	8 Days	10 Days	12½ Days	18 Days	56 Days
First regeneration	3690	9.7	0.48	1.0	1.7	2.4	2.6	2.7	2.2
	3709	8.8	0.48	1.3	2.0	2.6	3.2	3.4	3.3
	3727	8.3	0.48	1.1	1.6	2.0	2.2	2.2	2.2
	3745	10.0	0.54	1.8	2.4	3.8	4.4	4.8	4.2
	3744	6.0	0.36	1.0	1.3	1.7	1.8	1.7	—
	3761	6.6	0.39	1.0	1.5	1.9	2.2	2.3	1.8
	3763	8.5	0.57	1.1	1.8	2.4	2.9	3.1	—
	3689	6.3	0.30	0.7	1.2	1.5	1.6	1.7	1.4
	Average	8.2							
Second regeneration	3679	8.4	0.30	0.7	1.4	1.9	1.9	2.1	—
	3685	9.3	0.60	1.2	1.9	2.3	2.8	3.0	2.6
	3697	7.3	0.48	1.2	1.7	2.2	2.4	2.3	2.1
	3703	9.3	0.45	1.3	2.0	2.5	2.6	2.5	2.5
	3715	7.9	0.24	0.9	1.7	2.3	2.6	2.6	2.8
	3721	8.7	0.57	1.3	1.9	2.3	2.6	2.3	2.2
	3733	8.5	0.36	1.0	1.9	2.4	2.6	2.6	2.8
	3734	8.5	0.48	2.1	3.1	4.5	5.7	6.4	6.6
	3739	9.6	0.36	1.0	1.8	2.4	3.0	2.9	—
	3751	6.7	0.45	1.1	1.7	2.1	2.4	2.5	2.3
	3757	8.0	0.42	1.2	2.1	2.8	3.1	3.2	3.1
	Average	8.4							
Av. length—First regen.			0.45	1.1	1.7	2.3	2.6	2.7	2.5
Av. length—Second regen.			0.42	1.1	1.8	2.3	2.6	2.6	2.5
Increase or decrease			—0.03	0.0	+0.1	0.0	0.0	—0.1	0.0
Specific lg.—First regen.			0.05	0.13	0.21	0.28	0.31	0.33	0.30
Specific lg.—Second regen.			0.05	0.13	0.22	0.28	0.31	0.31	0.30
Increase or decrease			0.00	0.00	+0.01	0.00	0.00	—0.02	0.00

TABLE 25

Rana clamitans Series 3676-3765
Comparison of first and second regenerations Age factor eliminated
One-half of tail removed

	Catalog number	Removed length mm.	Length regenerated in mm.						
			4 Days	6 Days	8 Days	10 Days	12½ Days	18 Days	56 Days
First regeneration	3710	12.3	0.42	1.8	2.9	3.7	3.9	3.9	3.9
	3728	12.8	0.60	1.7	2.8	3.9	4.8	5.4	5.8
	3746	13.3	0.54	1.7	2.4	4.1	5.7	7.0	6.8
	3764	14.6	0.42	1.3	2.5	4.2	5.3	6.8	6.5
	3765	12.2	0.30	1.5	2.3	3.2	3.9	4.5	4.5
	Average	13.0							
Second regeneration	3686	14.5	0.60	2.1	3.4	4.8	5.3	5.2	—
	3698	14.9	0.50	1.5	3.3	4.3	5.0	5.4	5.4
	3704	14.5	0.45	2.2	3.3	4.4	5.2	5.5	5.4
	3716	12.7	0.39	1.7	2.4	3.4	4.2	5.1	4.4
	3722	12.5	0.60	1.6	2.6	3.6	3.9	3.5	4.2
	3740	13.9	0.30	1.1	2.1	3.0	4.6	5.6	6.8
	3752	12.2	0.54	1.7	2.5	3.4	4.1	4.0	—
	3758	11.0	0.60	1.5	2.2	2.9	3.6	4.1	4.9
	Average	13.1							
Av. length—First regen.			0.46	1.6	2.6	3.8	4.7	5.5	5.5
Av. length—Second regen.			0.50	1.7	2.7	3.7	4.4	4.8	5.2
Increase or decrease			+0.04	+0.1	+0.1	—0.1	—0.3	—0.7	—0.3
Specific lg.—First regen.			0.03	0.12	0.20	0.29	0.36	0.42	0.42
Specific lg.—Second regen.			0.04	0.13	0.21	0.28	0.34	0.37	0.40
Increase or decrease			+0.01	+0.01	+0.01	—0.01	—0.02	—0.05	—0.02

TABLE 26

Comparison of first and second regenerations Age factor eliminated
Rana clamitans Series 3676-3765
Two-thirds of tail removed

	Catalog number	Re-moved length mm.	Length regenerated in mm.						
			4 Days	6 Days	8 Days	10 Days	12½ Days	18 Days	56 Days
First regeneration	3692	16.8	0.51	1.1	2.2	3.2	4.3	5.0	5.2
	3693	17.2	0.48	1.8	3.3	5.0	6.5	7.3	6.6
	3711	17.0	0.54	1.8	3.6	5.6	7.0	7.7	8.3
	3729	16.1	0.48	1.9	3.3	4.6	5.5	6.7	6.4
	3749	16.2	0.54	1.2	2.7	4.2	5.6	7.1	7.8
	Average	16.7							
Second regeneration	3680	16.0	0.60	1.9	3.0	4.2	5.2	6.4	6.6
	3681	21.2	0.84	3.0	4.0	5.6	6.3	7.3	7.2
	3687	19.7	0.54	3.6	5.6	6.0	6.6	7.0	—
	3699	21.0	0.54	2.2	4.3	5.9	7.1	7.5	7.2
	3705	17.6	0.72	2.0	3.6	4.8	6.4	6.2	6.0
	3717	17.6	0.42	2.6	3.6	5.2	6.0	6.7	6.4
	3723	18.4	0.30	2.3	3.7	5.3	6.5	8.1	8.3
	3735	16.5	0.48	2.0	3.4	5.5	6.5	7.8	8.0
	3741	16.0	0.30	1.9	3.0	4.4	5.8	6.9	7.0
	3753	16.8	0.42	2.0	2.5	3.8	5.2	6.4	7.1
	Average	18.1							
Av. length—First regen.			0.51	1.56	3.02	4.52	5.78	6.76	6.86
Av. length—Second regen.			0.52	2.35	3.67	5.07	6.16	7.03	7.09
Increase or decrease			+0.01	+0.79	+0.65	+0.55	+0.38	+0.27	+0.23
Specific lg.—First regen.			0.03	0.09	0.18	0.27	0.35	0.40	0.41
Specific lg.—Second regen.			0.03	0.13	0.20	0.28	0.34	0.39	0.39
Increase or decrease			0.00	+0.04	+0.02	+0.01	—0.01	—0.01	—0.02

TABLE 27

Rana clamitans Series 3676-3765
Comparison of first and second regenerations Age factor eliminated
Average lengths regenerated in mm.

Approx. fraction of tail removed	Regeneration	Number of individuals	Average length removed in mm.	Average length regenerated in mm.						
				4 Days	6 Days	8 Days	10 Days	12½ Days	18 Days	56 Days
1/18	1	2	1.5	0.3	0.5	0.8	0.9	0.9	0.9	0.7
	2	4	1.5	0.2	0.6	0.9	1.0	1.0	1.0	0.9
1/10	1	5	2.6	0.1	0.5	0.7	1.0	1.2	1.1	1.1
	2	7	2.8	0.4	0.8	1.1	1.3	1.3	1.2	0.8
1/6	1	3	4.6	0.5	1.0	1.5	1.7	1.8	1.8	1.5
	2	5	4.9	0.2	0.7	1.2	1.4	1.6	1.5	1.6
1/3	1	8	8.2	0.4	1.1	1.7	2.3	2.6	2.7	2.5
	2	10	8.4	0.4	1.1	1.8	2.3	2.6	2.6	2.5
1/2	1	5	13.0	0.5	1.6	2.6	3.8	4.7	5.5	5.5
	2	8	13.1	0.5	1.7	2.7	3.7	4.4	4.8	5.2
2/3	1	5	16.7	0.5	1.6	3.0	4.5	5.8	6.8	6.9
	2	10	18.1	0.5	2.3	3.7	5.1	6.2	7.0	7.1

TABLE 28

Rana clamitans Series 3676-3765

Comparison of first and second regenerations Age factor eliminated
Specific lengths regenerated

Approx. fraction of tail removed	Re-generation	Number of individuals	Average length removed in mm.	Specific length regenerated in mm.						
				4 Days	6 Days	8 Days	10 Days	12½ Days	18 Days	56 Days
$^1/_{18}$	1	2	1.5	0.17	0.30	0.53	0.58	0.61	0.60	0.45
	2	4	1.5	0.15	0.42	0.60	0.67	0.67	0.67	0.60
$^1/_{10}$	1	5	2.6	0.06	0.18	0.27	0.38	0.46	0.42	0.42
	2	7	2.8	0.14	0.30	0.39	0.46	0.46	0.43	0.29
$^1/_6$	1	3	4.6	0.11	0.22	0.33	0.37	0.39	0.39	0.34
	2	5	4.9	0.05	0.14	0.24	0.29	0.33	0.31	0.33
$^1/_3$	1	8	8.2	0.05	0.13	0.21	0.28	0.31	0.33	0.30
	2	10	8.4	0.05	0.13	0.22	0.28	0.31	0.31	0.30
$^1/_2$	1	5	13.0	0.03	0.12	0.20	0.29	0.36	0.42	0.42
	2	8	13.1	0.04	0.13	0.21	0.28	0.34	0.37	0.40
$^2/_3$	1	5	16.7	0.03	0.09	0.18	0.27	0.35	0.40	0.41
	2	10	18.1	0.03	0.13	0.20	0.28	0.34	0.39	0.39
All levels—Average—First				0.075	0.173	0.287	0.362	0.413	0.427	0.390
All levels—Average—Second				0.077	0.208	0.310	0.377	0.408	0.413	0.385
First ahead				—	—	—	—	0.005	0.014	0.005
Second ahead				0.002	0.035	0.023	0.015	—	—	—

TABLE 29

Rana clamitans Series 3676-3765

Comparison of first and second regenerations Age factor eliminated

Difference between first and second regenerations

Approx. fraction of tail removed	Average length removed in mm.	Number of individuals			Increase—second over first regeneration						
		First regen.	Second regen.		4 Days	6 Days	8 Days	10 Days	12½ Days	18 Days	56 Days
$^{1}/_{18}$	1.5	2	4	Length in mm.	—0.1	+0.1	+0.1	+0.1	+0.1	+0.1	+0.2
				Specific length	—0.02	+0.12	+0.07	+0.09	+0.08	+0.07	+0.15
$^{1}/_{10}$	2.7	5	7	Length in mm.	+0.3	+0.3	+0.4	+0.3	+0.1	+0.1	—0.3
				Specific length	+0.08	+0.12	+0.12	+0.08	0.00	+0.01	—0.13
$^{1}/_{6}$	4.8	3	5	Length in mm.	—0.3	—0.3	—0.3	—0.3	—0.2	—0.3	+0.1
				Specific length	—0.06	—0.08	—0.09	—0.08	—0.06	—0.08	—0.01
$^{1}/_{3}$	8.3	8	10	Length in mm.	0.0	0.0	+0.1	0.0	0.0	—0.1	0.0
				Specific length	0.00	0.00	+0.01	0.00	0.00	—0.02	0.00
$^{1}/_{2}$	13.1	5	8	Length in mm	0.0	+0.1	+0.1	—0.1	—0.3	—0.7	—0.3
				Specific length	+0.01	+0.01	+0.01	—0.01	—0.02	—0.05	—0.02
$^{2}/_{3}$	17.6	5	10	Length in mm.	0.0	+0.7	+0.7	+0.6	+0.4	+0.2	+0.2
				Specific length	0.00	+0.04	+0.02	+0.01	—0.01	—0.01	—0.02

TABLE 30

Rana clamitans Series 3676-3765

Specific rates of first and second regenerations during each of the time periods

Approx. fraction of tail removed	Regeneration	Number of individuals	Average length removed in mm.	Specific rate of regeneration						
				0-4 Days	4-6 Days	6-8 Days	8-10 Days	10-12½ Days	12½-18 Days	18-56 Days
1/18	1	2	1.5	0.042	0.065	0.115	0.025	0.015	—0.002	—0.004
	2	4	1.5	0.037	0.135	0.090	0.035	0.000	0.000	—0.002
1/10	1	5	2.6	0.015	0.040	0.045	0.055	0.040	—0.007	—0.001
	2	7	2.8	0.035	0.080	0.045	0.035	0.000	—0.005	—0.004
1/6	1	3	4.6	0.027	0.055	0.055	0.020	0.010	0.000	—0.001
	2	5	4.9	0.012	0.045	0.050	0.025	0.025	—0.004	0.001
1/3	1	8	8.2	0.012	0.040	0.040	0.035	0.015	0.004	—0.001
	2	10	8.4	0.012	0.040	0.045	0.030	0.015	0.000	—0.000
1/2	1	5	13.0	0.007	0.045	0.040	0.045	0.035	0.011	0.000
	2	8	13.1	0.010	0.045	0.040	0.035	0.030	0.005	0.001
2/3	1	5	16.7	0.007	0.030	0.045	0.045	0.040	0.009	+0.000
	2	10	18.1	0.007	0.050	0.035	0.040	0.030	0.009	0.000
All levels—Average—First				0.018	0.046	0.057	0.037	0.026	0.002	—0.001
All levels—Average—Second				0.019	0.066	0.051	0.033	0.017	0.001	—0.001
First ahead				——	——	0.006	0.004	0.009	0.001	——
Second ahead				0.001	0.020	——	——	——	——	——

EXPERIMENT III AMBLYSTOMA PUNCTATUM SERIES 3962-3999

Material and Method Eggs of Amblystoma punctatum in the cleavage stages were collected on March 18, 1913, and hatched in the laboratory on April 9. The first operations were made on April 23, at which time also five controls were killed and preserved. These when measured gave an average total length of 13.1 mm. and an average tail length of 5.3 mm. Ninety individuals were used for the regeneration study. In thirty individuals two-thirds in length of the tail was removed on April 23. The regenerated portion in these was removed on May 10 and at the same time in a second thirty individuals two-thirds of the tail was removed. On May 21 the first thirty were operated on for the third time, the second thirty for the second time, and the third thirty for the first time. To insure as accurate a comparison as possible the ninety individuals though they were approximately of equal size were divided into thirty groups of three each, a selection being made so that the three members of a group were as much alike as possible. In each group one of the three members was used for the first regeneration, one for the second and the third for the third regeneration. This procedure gave a possibility of comparing the first, second and third regenerations without error due to difference in size, age, or in external conditions.

Three individuals from each thirty were killed two days after the last operations, four in four days, five in six days, five in eight days, six in ten days and seven in fourteen days.

At the end of the experiment, control individuals gave an average total length of 31.5 mm. and an average tail length of 10.5 mm.

Data The data are given in Tables 31 and 32. The specific amounts of regeneration were not determined because the removed lengths were alike and hence the comparison of absolute lengths gives the same results as a comparison of specific amounts.

The average regenerated lengths at each of the six different times will be taken up first. At two days the average regenerated lengths for the first, second and third regenerations are respectively 0.22, 0.25 and 0.26 mm. At four days the corresponding amounts are 0.66, 0.75 and 1.00. At six days they are 1.36, 1.40 and 1.36, but the low value of the third regeneration is due to a single exceptional individual. At eight days the figures are 2.18, 2.68 and 2.68. At ten days they are 3.55, 3.82 and 4.20 and at fourteen days 5.34, 6.12 and 6.08. In all cases, except the one at six days explained above, both second and third regenerations are ahead of the first. The third regeneration is greater than the second at two, four and ten days, is equal to the second at eight days and less than the second at six and fourteen days. Since the low average for the third regeneration at six days is due to a single exceptional individual it is more proper to put the third ahead of the second at this time.

A comparison of the three regenerations by individual cases is shown in Table 32. At each of the six times taken the number of cases showing a more rapid regeneration is greater for the third regeneration than for the first and also greater for the second than for the first. The third is ahead of the second at two times (more properly three times) and equal to the third at four times (more properly three).

When all the individual cases are taken together both third and second regenerations are again distinctly ahead of the first as shown by the totals in Table 32. The third is ahead of the second in twelve cases (more properly thirteen) and the second ahead of the first in eight cases (more properly seven).

Each of the three comparisons shows that both second and third regenerations are more rapid than first regenerations. The third regeneration shows a slight advantage over the second instance in all three of the comparisons. In this instance the difference can not be due to the presence of newly regenerated cells in the one case and not in the other.

TABLE 31

Amblystoma punctatum Series 3967-3998
Comparison of lengths of first, second and third regenerations
Age factor eliminated

Regeneration time in days	Catalog number	Regenerated lengths in mm.		
		First regeneration	Second regeneration	Third regeneration
2	3967	0.2	0.25	0.3
	3968	0.25	0.3	0.27
	3969	0.2	0.2	0.2
	Average	0.22	0.25	0.26
4	3970	0.75	0.9	1.0
	3971	0.7	—	1.6
	3972	0.5	0.75	0.8
	3973	0.7	0.6	0.6
	Average	0.66	0.75	1.00

TABLE 31 (Continued)
Amblystoma punctatum Series 3967-3998
Comparison of lengths of first, second and third regenerations
Age factor eliminated

Regeneration time in days	Catalog number	Regenerated lengths in mm.		
		First regeneration	Second regeneration	Third regeneration
6	3974	1.2	1.2	—
	3975	1.4	1.5	1.5
	3976	1.3	1.4	1.6
	3977	1.5	1.2	0.6
	3978	1.4	1.7	1.7
	Average	1.36	1.40	1.36
8	3980	1.7	2.4	2.7
	3981	1.9	—	2.9
	3982	2.3	2.6	3.0
	3984	2.4	2.8	2.1
	3985	2.6	2.9	2.7
	Average	2.18	2.68	2.68
10	3986	4.1	3.8	4.7
	3987	3.6	3.7	—
	3988	3.5	—	3.9
	3989	2.6	3.9	3.5
	3990	3.2	4.25	4.6
	3991	4.3	3.5	4.35
	Average	3.55	3.82	4.20
14	3992	5.5	5.5	5.7
	3993	5.0	5.75	5.7
	3994	—	6.7	6.9
	3995	5.0	5.7	6.9
	3997	6.9	6.7	5.2
	3998	4.3	6.35	—
	Average	5.34	6.12	6.08

TABLE 32

Amblystoma punctatum Series 3967-3998 Age factor eliminated
Comparison of lengths of first, second and third regenerations
Comparison of individual cases

Comparisons	Two days	Four days	Six days	Eight days	Ten days	Fourteen days	Totals
3rd regen. > 1st	2	3	3	4	5	3	20
3rd regen. = 1st	1	0	0	0	0	0	1
3rd regen. < 1st	0	1	1	1	0	1	4
2nd regen. > 1st	2	2	3	4	3	3	17
2nd regen. = 1st	1	0	1	0	0	1	3
2nd regen. < 1st	0	1	1	0	2	1	5
3rd regen. > 2nd	1	2	1	2	3	3	12
3rd regen. = 2nd	1	1	2	0	0	0	4
3rd regen. < 2nd	1	0	1	2	1	3	8

EXPERIMENT IV AMBLYSTOMA PUNCTATUM SERIES 3962-3999

The series used for Experiment III furnishes another set of data for the effect of successive removal. When the third operation was made the removed regenerated tails of the first thirty individuals represented an eleven-day second regeneration and those of the second thirty-individuals an eleven-day first regeneration. A direct comparison is thus possible between the first and the second regenerations. It is not possible to make a cut exactly at the border line between old and new tissue and therefore the measurement of the removed regenerating tail is not as accurate a determination as is the direct measurement of a regenerating unremoved tail.

The data are shown in Table 33. Twenty-five individuals are available for each regeneration. The average of the first regenerations is 4.55 ±0.11 and of the second regenerations 4.50 ±0.10. The first regeneration is ahead of the second in ten cases, the second is ahead of the first in twelve cases and three cases are equal. The first comparison shows a slight difference in favor of the first regeneration but this is so much less than the probable error that it can not be considered as significant. The second comparison shows a slight advantage in favor of the second regeneration. On the whole the data indicate essential equality between the first and the second regenerations at eleven days.

TABLE 33

Amblystoma punctatum Series 3962-3999 Age factor eliminated
Comparison of first and second regenerations
Eleven days

Catalog number	First regen. mm.	Second regen. mm.	First ahead of second	Second ahead of first	First and second equal
3967	4.0	4.4		0.4	
3968	3.7	3.5	0.2		
3969	4.9	5.1		0.2	
3970	4.5	4.7		0.2	
3972	4.7	4.7			*
3973	3.9	4.3		0.4	
3975	4.5	5.7		1.2	
3976	4.9	4.9			*
3977	3.8	3.7	0.1		
3978	4.1	4.5		0.4	
3980	4.9	5.0		0.1	
3981	3.5	4.4		1.1	
3982	5.0	4.7	0.3		
3984	5.1	4.0	1.1		
3985	5.8	4.3	1.5		
3986	3.8	4.1		0.3	
3989	4.8	5.5		0.7	
3990	5.5	4.3	1.2		
3991	4.1	4.6		0.5	
3992	4.6	4.1	0.5		
3993	4.5	4.5			*
3994	4.9	5.0		0.1	
3995	4.5	4.0	0.5		
3997	5.1	4.2	0.9		
3998	4.8	4.3	0.5		
	4.55±0.11	4.50±0.10	ten times	twelve times	three times

Experiment V Amblystoma punctatum Series 6042-6100F

This series was devised for a study of the effect of repeated removal of the tail upon the rate of metamorphosis. The removed tails were preserved and they give some data on the comparison of successive regenerations. The interest of the results lies in the fact that the successive regenerations are compared within single individuals. Thus the effect of the age factor is not eliminated. Environmental differences such as those of temperature may also be factors.

The eggs were hatched on March 25 to 29, 1915. Approximately one-half in length of the tail was removed in each of the individuals on April 5. The new tissue was removed on April 17 and again on May 1, May 10 and May 19, making five removals in all. The second removal gives the first regeneration, the third the second, and so on. The regenerated lengths were therefore determined by measurement of removed parts. This does not give as accurate a determination as does direct measurement without removal because the cut can not in ordinary practice be made exactly at the border line between old and new tissue.

The data are given in Table 34. The first regeneration covers a twelve-day period, the second fourteen days and the third and fourth each nine days.

The third and fourth regenerations are the only ones that have the same time interval. Ten individuals are available for this comparison. The average for the third regeneration for these ten is 1.30 mm. and of the fourth regeneration 1.17 mm. When all individuals are taken without regard to representation of both regenerations the average for the third regeneration is 1.28 and for the fourth 1.17. In seven of the ten former cases the third is ahead of the fourth regeneration, in two they are tied and in one the fourth is ahead of the third. The data therefore show an advantage of the third over the fourth regeneration.

The first regeneration ran twelve days and the second fourteen days. The maximum rate of regeneration comes on or near the ninth day and the rate has declined to a low point by the fourteenth day. However it is not possible to make the necessary correction because of lack of data on the rate curve for this particular set of larvae. Some facts may however be obtained by a comparison. Sixteen individuals for each of the two regenerations are available for comparison. The average for the first regeneration in these is 2.06 mm. and for the second 2.01 mm. In seven the first is ahead of the second, in seven the second is ahead of the first, and two are tied. When all individuals are taken without regard to representation of both regenerations the average for the first regeneration is 1.99 ±0.03 mm. for a twelve-day period and for the second regeneration 2.01 for a fourteen-day period. The difference between the two values is not significant, but when the longer time interval taken by the second regeneration is considered the conclusion is reached that the first regeneration is more rapid than the second.

The data thus indicate a progressive decrease in rate from the first to the fourth regenerations. This result taken in connection with the results obtained from the experiments in which the age factor is eliminated makes it highly probable that the decrease in rate of regeneration observed here is due to increase in age and not to the effect of successive removal.

TABLE 34

Amblystoma punctatum Series 6042-6100 F Age factor eliminated
Successive regenerations in single individuals

Catalog number	First regeneration mm.	Second regeneration mm.	Third regeneration mm.	Fourth regeneration mm.
	Twelve days	Fourteen days	Nine days	Nine days
6042	2.0	2.4	1.6	
6043	1.8	2.5	1.5	1.4
6044	2.2			
6046	2.2	2.2	1.3	1.3
6047	2.2	2.1	1.4	1.3
6048	2.0	2.2		
6049	2.3	1.8	1.5	1.0
6050	1.8			
6052	2.0			
6053	1.9			
6055	1.9			
6056	1.7			
6057	2.0			
6058	2.0			
6059	1.9			
6061	1.5			
6062	2.3			
6065	1.5			
6067	1.6			
6068	1.6			
6071	2.0			
6072	1.9			
6076	2.1			
6077	2.0			
6079	2.0			
6080	1.8			
6081	1.9			
6082	1.9	2.0	1.0	1.1
6083	2.0	2.1	1.3	1.1
6084	1.9			
6085	2.0	2.0	1.5	1.5
6086	2.2			
6087	1.8	1.0	0.8	
6088	2.1	2.4	1.4	1.2
6090	2.5			
6093	2.3	2.2	1.0	0.8
6094	2.1			

TABLE 34 (Continued)

Catalog number	First regeneration mm.	Second regeneration mm.	Third regeneration mm.	Fourth regeneration mm.
	Twelve days	Fourteen days	Nine days	Nine days
6096	2.1			
6097	2.5	1.6		
6098	1.8	2.1		
6099	2.2			
6100D	2.0			
6100E	1.8	1.6		
6100F	2.2	2.0	1.1	1.0
Average	**1.99±0.03**	**2.01**	**1.28**	**1.17**
Rate per day	**0.166**	**0.144**	**0.142**	**0.130**

EXPERIMENT VI BUFO AMERICANUS SERIES 6283-6323

This series was designed for the study of the effect of successive removal of the tail upon the rate of metamorphosis. The lengths of the removed regenerating tails however are of some value in a comparison of successive regenerations though here as in Experiment V age and external factors are not eliminated.

The eggs were laid on April 20-21, 1915. The tadpoles were collected on April 27 and the first removals were made on April 28. The first metamorphosis was completed on June 11. The average total length at the time of the first removal was 10.9 mm. and the average tail length 6.4 mm. The average removed length was 3.8 mm., which is approximately 60 per cent of the tail length. The second removal was made on May 7 and gives a nine-day period for the first regeneration. The third removal of May 17 gives a ten-day period for the second regeneration. The fourth removal on May 26 gives a nine-day period for the third regeneration. As in the case of Experiment V the cuts could not in practice be made to come exactly at the border line between old and new tissue and the accuracy of the measurements is therefore not as great as in those cases in which the lengths were taken directly from the animal without removal of the tail.

The data are shown in Table 35. The first, second and third regeneration lengths are given for sixty individuals. The first and third regenerations have the same time interval and are therefore directly comparable. The average for the first regeneration is 1.94 ±0.02 mm.

and for the third 1.80 ±0.03 mm., a difference in favor of the first regeneration of 0.14 ±0.05 mm. This represents a regeneration of 0.51 mm. per unit of removed length in the first regeneration and 0.47 mm. per unit in the third regeneration. A comparison of individual cases shows that the first regeneration is ahead of the third in 36 individuals, the third is ahead of the first in 18 individuals and 5 are tied. The difference between the two regenerations is thus probably significant. As in Experiment V the decrease is probably due to the age factor.

The second regeneration has a time interval of ten days, one day more than the first and third regenerations. In the absence of knowledge concerning the rate curve for toad tadpoles of this age no correction can be applied. The rates per day for the three regenerations are however given in the table.

TABLE 35

Bufo americanus Series 6283-6323 Age factor not eliminated

Successive regenerations of tail

Catalog number	First regeneration Nine days Length in mm.	Second regeneration Ten days Length in mm.	Third regeneration Nine days Length in mm.
6283 a	2.1	2.0	1.9
b	1.5	2.1	1.6
c	1.7	2.1	1.7
6285 a	2.3	1.9	2.0
b	2.3	2.1	2.0
c	2.0	2.4	2.4
6287 a	1.9	2.1	2.1
b	2.1	2.0	1.9
c	1.8	2.3	1.8
6289 a	1.9	2.3	2.2
b	2.1	2.0	1.7
c	2.2	2.1	2.0
6291 a	2.1	2.2	2.0
b	1.9	1.9	1.8
c	2.0	1.9	1.4
6295 a	2.0	2.0	2.0
b	2.1	2.1	1.8
c	1.8	1.9	1.9
6297 a	1.9	2.0	2.0
b	1.9	2.1	1.8
c	1.9	2.0	1.8
6299 a	1.8	2.0	1.5
b	2.0	2.0	1.7

TABLE 35 (Continued)

Catalog number	First regeneration Nine days Length in mm.	Second regeneration Ten days Length in mm.	Third regeneration Nine days Length in mm.
c	1.8	1.9	1.3
6301 a	2.0	1.5	1.4
b	1.8	1.9	1.2
c	1.7	1.8	1.4
6303 a	1.9	1.9	1.3
b	1.9	1.9	1.5
c	1.8	2.0	1.6
6305 a	1.9	2.0	1.5
b	1.7	1.8	2.0
c	2.1	2.2	1.9
6307 a	2.1	1.8	2.0
b	1.9	2.0	2.1
c	1.8	1.9	1.8
6309 a	2.0	1.9	1.9
b	1.9	1.9	2.0
c	2.0	2.0	1.7
6311 a	1.7	2.4	1.8
b	1.8	1.9	2.1
c	2.0	2.1	2.0
6313 a	2.0	2.3	1.7
b	1.8	1.7	2.0
c	1.7	1.7	1.5
6315 a	1.9	2.4	2.0
b	2.0	2.1	1.6
c	..	1.9	1.9
6317 a	1.9	2.0	1.3
b	1.8	2.2	2.0
c	1.9	2.1	1.8
6319 a	2.2	2.0	2.0
b	2.1	2.0	2.0
c	1.9	1.9	2.0
6321 a	2.3	2.0	1.8
b	1.7	2.0	1.9
c	2.0	2.3	1.3
6323 a	2.1	2.1	1.7
b	1.8	2.3	2.0
c	1.9	2.2	2.0
Average	**1.94±0.02**	**2.02±0.02**	**1.80±0.03**
Rate per day	**0.216**	**0.202**	**0.200**

EXPERIMENT VII RANA CLAMITANS SERIES 3557-3624

This experiment deals with the relative completeness of regeneration after successive removals within single individuals. Age and external factors are not eliminated. A more complete description of the experiment is given under "Completeness of Regeneration." The tail length averaged approximately 17.0 mm. About one-half of the tail was removed at the first operation. At succeeding operations the cut came as near as possible to the border line between old and new tissue. The first removals came on October 23, 1911, the second on November 28, the third January 3, the fourth February 9, the fifth March 16 and the sixth April 4. At the time of the last removal the hind legs were just starting to grow.

The data are given in Table 36. The first regeneration interval is 36 days, the second 36, the third 37, the fourth 36 and the fifth 39 days. Each one of these is more than sufficient for the completion of the regenerative process. The individuals are divided into three sets, A, B, and C. A, with seven individuals, has no record for the first regeneration; the second regeneration is 9.8 mm., the third 9.3, the fourth 8.5 and the fifth 8.6. B, also with seven individuals, has no record for the first regeneration; the second is 9.1 mm., the third 8.9, the fourth 7.2 and the fifth 7.8. C, with nineteen individuals, has a first regeneration average of 8.6 mm., a second of 8.0, a third of 7.5, a fourth of 5.5 and a fifth of 6.4. In all the cases there is a decrease in the amount regenerated with successive removal except for the fifth regeneration, which has in each case an increase over the fourth. It is probable that

TABLE 36

Rana clamitans Series 3564-3624 Age factor not eliminated
Completed successive regenerations compared

Set	Catalog number	Number of individuals	First regeneration 36 Days	Second regeneration 36 Days	Third regeneration 37 Days	Fourth regeneration 36 Days	Fifth regeneration 39 Days
A	3564 to 3570	7	..	9.8	9.3	8.5	8.6
B	3578 to 3584	7	..	9.1	8.9	7.2	7.8
C	3586 to 3624	19	8.6	8.0	7.5	5.5	6.4

the decrease is due to increase in age. The increase from the fourth to the fifth regeneration may be due to some special characteristic of the stage immediately preceding metamorphosis or it may merely indicate the existence of some uncontrolled external factor such as food or temperature.

DISCUSSION

The evidence shows clearly that when the age factor is eliminated there is no decrease in rate of regeneration with successive removal. On the contrary the second regeneration is more rapid than the first up to the period of maximum rate. The second regeneration however passes its maximum sooner than does the first and after the tenth day the latter therefore catches up to the former in total amount regenerated. There is no striking difference between the second and the third regenerations but in each comparison the third has a slight advantage.

When the successive regenerations in single individuals are compared, the rate decreases with successive removal. This decrease is undoubtedly due to the age factor.

The possibility has suggested itself that the second regeneration starts out at a more rapid rate than the first because the cells at the cut surface were undergoing regenerative changes at the time of the new operation and can therefore start the process much faster than can the old cells at the first surface of regeneration. Following a first removal there is a considerable degree of reorganization of the cells at the cut surface, accompanied by active migration. During this period, which in *Rana clamitans* lasts two or three days, there is little or no mitotic cell division. Then follows a division period which reaches its maximum at seven to ten days. Its decline is associated with the oncoming of tissue differentiation (Sutherland 1915, Metcalf 1915).

A special study has been made of the relative rates of second regenerations from old cells following a cut inside of the first removal level and from new cells following a cut outside of the first level. This comparison shows only a very slight difference in favor of the new cells and this is largely confined to the early stages, the period of cell migration.

The period of increase in rate is the period of active cell multiplication and the decline in rate is associated with cell differentiation. The second regeneration therefore reaches the period of differentiation slightly in advance of the first regeneration.

Apart from the slowing due to age there is no indication of a limitation of the amount of new material that may be produced by regeneration. The actual limitation comes not from the using up of regenerative or developmental energy or of determiners by repeated regeneration but from changes in the non-regenerating part associated with age. In another place there is a discussion of the possibility that there may be an effect upon the rate of developmental processes in the organism as a whole due to continued regeneration of a part. This is studied particularly in connection with the effect of regeneration upon rate of metamorphosis in Amphibia.

Regeneration studies in general and those on successive regeneration in particular make it improbable that there is a definite number of cell generations between the fertilized egg and the end product, the differentiated cells. The possibility that certain cells may remain in an early cell generation can not be wholly excluded as an explanation of at least a part of first regeneration phenomena. Under suitable stimulation such cells may be postulated to take up development where it had left off. The definite descriptions of de-differentiations of cells as well as other facts of regeneration argue against this conclusion. The view that there can be no such definite number of cell generations is strengthened by the facts of successive regeneration. It does not seem probable that embryonic cells of an early cell generation can be held in reserve through repeated regenerations.

The explanation of regeneration by the theory of duplicate sets of determiners meets difficulties in undiminished successive regenerations. The greater the number of repeated regenerations the greater the difficulties of explanation on this basis. Of course the difficulty does not hold for the hypothesis that every cell or nearly every cell contains a full set of determiners.

The earlier appearance of the maximum rate in the second than in the first regeneration may be due to the more rapid progress of the cells in the early cell migration period alone or it may be due to the acceleration of the whole developmental cycle.

Summary

1. The age factor was eliminated in Experiments I to IV. Experiments I and II deal with tadpoles of Rana clamitans and Experiments III and IV with larvae of Amblystoma punctatum.

2. In Experiment I approximately one-half of the tail was removed. At six days the average first regeneration length is 2.01 mm. and the average second regeneration length 2.18 mm. In five cases the first exceeds the second and in six the second exceeds the first. The corresponding specific lengths are 0.194 and 0.205. The first regeneration exceeds the second in two sets, the second exceeds the first in eight and one is tied. The second regeneration has the advantage in all the comparisons.

3. At eight days in Experiment I the average first regeneration length is 3.06 mm., and the second 3.42 mm. The first exceeds the second in three sets and the second exceeds the first in seven. The corresponding average specific lengths are 0.298 and 0.323. In four sets the first regeneration exceeds the second and in six the second exceeds the first. The second regeneration has the advantage in all the comparisons.

4. The advantage of the second regeneration over the first in Experiment I holds true of second regenerations from both old tissue and new tissue levels.

5. In Experiment II observations were made at the 1/10, 1/3, 1/2 and 2/3 levels in a sufficient number of individuals to yield valid data. Regeneration measurements were made at each of these levels 4, 6, 8, 10, 12½, 18 and 56 days after the operations. The second regeneration at all of them tends to be ahead of the first until the tenth day, after which the first regeneration catches up. The maximum rate for both regenerations is reached before this time and earlier for the second than for the first regeneration.

6. In Experiment III two-thirds of the tail was removed. A comparison of the first, second and third regenerations was made at 2, 4, 6, 8, 10 and 14 days.. At two days the first, second and third regenerations average respectively 0.22, 0.25 and 0.26 mm. The corresponding values at four days are 0.66, 0.75 and 1.00; at six days 1.36, 1.40 and 1.46; at eight days 2.18, 2.68 and 2.68; at ten days 3.55, 3.82 and 4.20; at fourteen days 5.34, 6.12 and 6.08. The advantage is in favor of the second and third regenerations as opposed to the first and of the third as opposed to the second. Individual comparisons at each of the different times as well as in the experiment as a whole show the same results.

7. The removed tails in the preliminary procedure of Experiment III furnish the data of Experiment IV and allow a comparison of the first and second regenerations at eleven days. The procedure is however subject to greater error than that of Experiments I to III. Twenty-five individuals for each regeneration give an average of 4.55 ±0.11 mm. for the first regeneration and 4.50 ±0.10 mm. for the second regeneration. The first regeneration is ahead of the second in ten cases, the second ahead of the first in twelve cases and three are equal. The two regenerations must be considered as essentially equal.

8. In Experiments V and VI the age factor is not eliminated. Successive regenerations in single individuals are compared. In Experiment V one-half of the tail in Amblystoma larvae was removed. In Experiment VI 60 per cent of the tail of toad tadpoles was removed.

The time intervals vary somewhat in each set but it is evident in both cases that there is a decrease in rate of regeneration from the first to the third and fourth regenerations. This decrease is undoubtedly due to increase in age and not to successive removal.

9. In Experiment VII a comparison of the completeness of regeneration in single individuals of *Rana clamitans* shows a progressive decrease in amount regenerated from the first to the fourth regeneration and an increase from the fourth to the fifth. In this experiment also the age factor is not eliminated and the decrease is probably due to increase in age.

PART III

THE EFFECT OF LEVEL OF THE CUT UPON THE RATE AND COMPLETENESS OF REGENERATION

The present study gives a description of some experiments made to define more accurately than has been done the exact relation between the level of the cut and rate of regeneration and especially the relation of this factor to the other factors affecting rate and completeness of regeneration. The factor is one of great interest because if it is true that the ratio between length regenerated per unit time and length removed is a constant it follows that no matter how much material is removed regeneration is always completed in the same time. It is therefore of great interest to determine the extent to which this statement is true, to analyze the elements of the level factor and to determine its relation to other factors.

EXPERIMENT I RANA CLAMITANS SERIES 3676-3765

The tadpoles were collected on December 9, 1911, and first removals were made in two-thirds of the individuals on December 22. A second removal was made in these individuals on January 8, and at the same time a first removal in the other one-third. Measurements were made four, six, eight, ten, twelve and a half, eighteen and fifty-six days after the operations of January 8. The first and second regenerations are treated separately and the second regenerations are taken up first because they have a larger number of individuals and therefore give the more uniform results.

SECOND REGENERATIONS

The different amounts removed approximate 6, 10, 18, 31, 49 and 67 per cent of the tail length. There are four individuals at the lowest removal, averaging 1.5 mm., seven at the next, averaging 2.8 mm., five at the third with an average of 4.9 mm., ten at the fourth with 8.4 mm., eight at the fifth with 13.1 mm., and ten at the sixth with 18.1 mm. The data are given in tables 37 to 40 and in graphic form in figures 4 to 17.

The regenerated lengths at ten days will be taken up first because at this time the period of maximum rate has been passed and its full effect is represented. Differentiation of the tissues has begun but there is still a considerable production of new cells by mitotic division except in the individuals with the two shortest removals in which the process is completed. The regenerated lengths for the six levels beginning with the shortest removal are respectively 1.0, 1.3, 1.4, 2.3, 3.7 and 5.1 mm. The data are given in the last two columns of table 37. There is very distinctly an increase in regenerated length with increase in removed length. Dividing the regenerated length by the removed length at each level, the fractions obtained are

$$\frac{1.0}{1.5}, \quad \frac{1.3}{2.8}, \quad \frac{1.4}{4.9}, \quad \frac{2.3}{8.4}, \quad \frac{3.7}{13.1}, \quad \text{and} \quad \frac{5.1}{18.1},$$

which give the specific regenerated lengths or lengths regenerated per unit of removed lengths. These values are 0.67, 0.46, 0.29, 0.28, 0.28 and 0.28. They show a remarkable constancy for removed lengths of 4.9 mm. and over. The relations between removed lengths and regenerated lengths are further shown in figure 4 which gives the removed lengths along the horizontal axis and the regenerated lengths parallel to the vertical axis. The plotted line of correlation between the two values is straight except for the two lowest removed lengths. The specific lengths are given in Figure 5 in which the removal lengths again are along the horizontal axis and the lengths regenerated per unit of removed length parallel to the vertical axis. The line of correlation is straight and parallel to the horizontal axis for the four highest removals. For these therefore the regenerated length is directly proportional to the removed length or in other words within these limits the same percentage of the removed length is regenerated in each within the given time of ten days.

The two lowest removed lengths give a higher specific rate than the others. They regenerate a higher percentage of the removed length within the given time.

The ten day period is chosen as the first example because it is the first one to receive the full benefit of the periods of maximum rate of regeneration, the periods during which rapid multiplication of cells takes place. The other periods give results which agree in general features after the first few days with those at ten days but depart from them in certain respects.

The remaining periods will now be taken up in turn beginning with the shortest.

During the first four days after the operation the rate of regeneration is slow, the new tissue being derived largely from migration of cells over the cut surface. Measurements of regeneration at this time are especially subject to error because of the small amount regenerated and because of irregularity in the outer edge of the regenerating tissue. The regenerated lengths at four days are respectively 0.22, 0.39, 0.24, 0.42, 0.50 and 0.52 mm. These data are given in table 37 and are represented graphically in figure 6. Dividing the regenerated lengths by the removed lengths the fractions obtained are

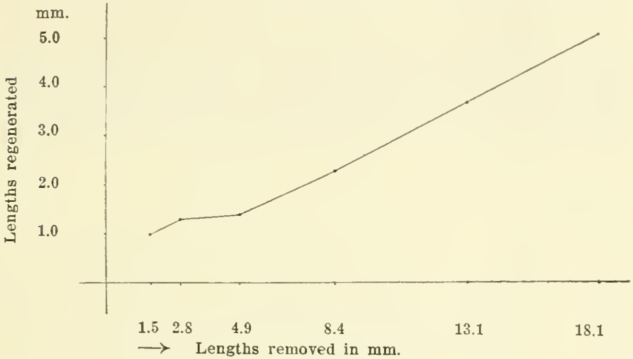

Figure 4 *Rana clamitans* Second regenerations Ten days

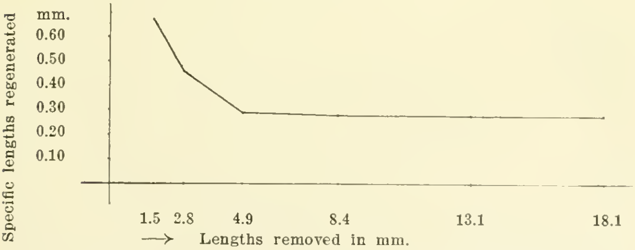

Figure 5 *Rana clamitans* Second regenerations Specific lengths Ten days

$$\frac{0.22}{1.50},\quad \frac{0.39}{2.80},\quad \frac{0.24}{4.90},\quad \frac{0.42}{8.40},\quad \frac{0.50}{13.10}\quad \text{and}\quad \frac{0.52}{18.10}$$

giving specific lengths of 0.15, 0.14, 0.05, 0.05, 0.04 and 0.03. These relations are represented graphically in figure 7. There is on the whole a slight increase in regenerated length with increase in removed length but this increase is not proportional to the amount removed so that the proportion regenerated decreases with increase in removed length. The approach to equality in regeneration at this time is probably due to the fact that the new tissue is largely made up of migrating cells and there is not a striking difference in the extent of the migration at the different levels.

The specific length of material regenerated after the smallest removals is greater than that regenerated after the larger removals not only at four days but also later. It is probable that the factors involved during the first few days of regeneration are quite different from those during later days. Following the injury there is a disintegration of injured cells associated with an active migration of the epidermal cells over the cut surface. There is practically no mitotic cell division. The rapid multiplication of cells comes later. These processes of cell migration apparently are not essentially different at the different levels. They are local responses of the cells at the cut surface. With the appearance of rapid cell multiplication there is a marked difference at different levels though the shortest removals still show a greater specific length than the others probably because in their case the migrated cells make up a large percent of the total material of the new part.

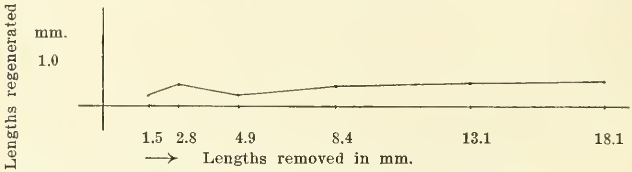

Figure 6 *Rana clamitans* Second regenerations Four days

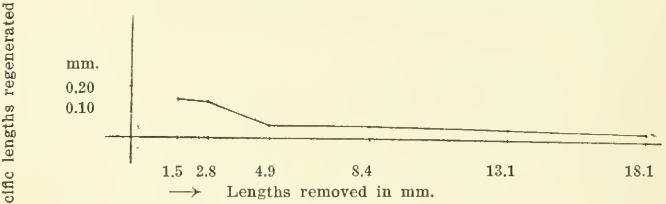

Figure 7 *Rana clamitans* Second regenerations Specific lengths Four days

Between the end of the fourth and the end of the sixth day after the operation mitotic cell division becomes very rapid and the rate of regeneration for second regenerations reaches its maximum at a majority of the levels on the sixth day. At six days the regeneration for the six levels is respectively 0.62, 0.80, 0.70, 1.1, 1.7 and 2.3 mm., as shown in

Table 37. A graphic representation is given in Figure 8. There is a gradual increase with increase in removed length. The fractions obtained by dividing by the removed lengths are:

$$\frac{0.62}{1.5},\quad \frac{0.80}{2.8},\quad \frac{0.70}{4.9},\quad \frac{1.1}{8.4},\quad \frac{1.7}{13.1}\quad \text{and}\quad \frac{2.3}{18.1}$$

They give specific lengths of 0.42, 0.30, 0.14, 0.13, 0.13 and 0.13. The smaller removals still have the larger specific lengths but with removals of 4.9 mm. and more there is an approach to constancy. The relations are shown graphically in Figure 9.

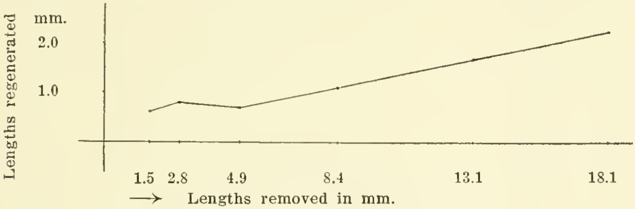

Figure 8 *Rana clamitans* Second regenerations Six days

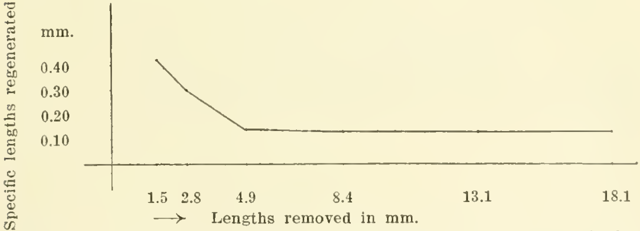

Figure 9 *Rana clamitans* Second regenerations Specific lengths Six days

The rate of regeneration between the sixth and the eighth day for second regenerations is not quite as high as for the preceding period, but mitotic divisions are still very numerous and differentiation of the cells is just beginning. At eight days the regenerated lengths are respectively 0.9, 1.1, 1.2, 1.8, 2.7 and 3.7 mm. as shown in table 37. The increase in regeneration with increase in removed length is evident. The relations are shown in Figure 10. Dividing by the removed lengths the fractions obtained are

$$\frac{0.9}{1.5},\quad \frac{1.1}{2.8},\quad \frac{1.2}{4.9},\quad \frac{1.8}{8.4},\quad \frac{2.7}{13.1}\quad \text{and}\quad \frac{3.7}{18.1}$$

giving the specific regenerations 0.60, 0.39, 0.24, 0.22, 0.21, 0.20. There is a graphic representation in Figure 11. As before, the two shortest removals give the highest specific rates but beyond these there is an approach to constancy though there is still a slight decrease with increase in removal.

The ten day values have already been given.

Between ten and twelve and a half days after the operation there is no further growth in the case of the two shortest removals. In the two medium removals the process is completed at twelve and a half days. In the two longest removals there is still a small amount of proliferation after this time. At twelve and a half days the regenerated lengths are 1.0, 1.3, 1.6, 2.6, 4.4 and 6.2 mm. as shown in Table 38. The increase with increase in removed length is continuous. This is shown

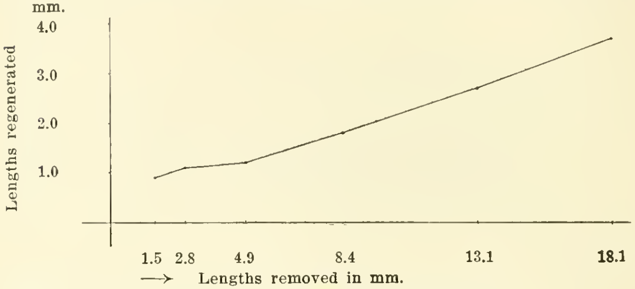

Figure 10 *Rana clamitans* Second regenerations Eight days

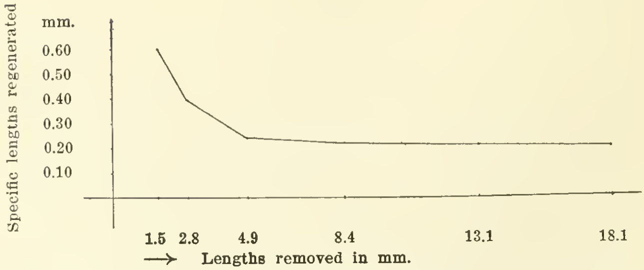

Figure 11 *Rana clamitans* Second regenerations Specific lengths Eight days

in graphic form in figure 12. Dividing by the removed lengths the fractions obtained are

$$\frac{1.0}{1.5}, \quad \frac{1.3}{2.8}, \quad \frac{1.6}{4.9}, \quad \frac{2.6}{8.4}, \quad \frac{4.4}{13.1} \quad \text{and} \quad \frac{6.2}{18.1}$$

giving specific lengths of 0.67, 0.46, 0.33, 0.31, 0.34 and 0.34. The graph for specific lengths is shown in figure 13. There is still a fair approach to constancy with removals of 4.9 mm. and above. The relative increase in the case of the higher removals is due to the fact that regeneration is continuing in them after it has stopped in the others.

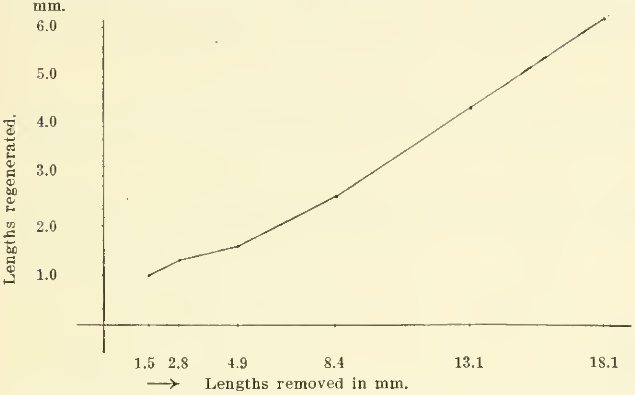

Figure 12 *Rana clamitans* Second regenerations Twelve and a half days

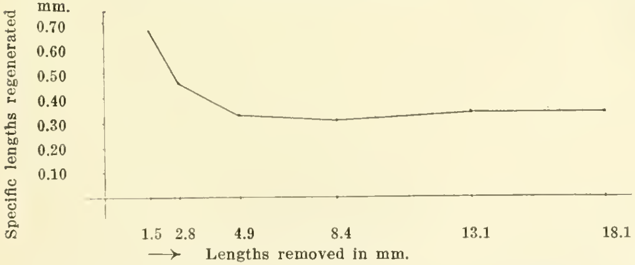

Figure 13 *Rana clamitans* Second regenerations Specific lengths Twelve and a half days

Therefore the data after this time are values for the completeness of regeneration rather than for the rate.

Between twelve and a half and eighteen days after the operation there is no further regeneration in the tails with the four shortest removals. Two of them even exhibit a decrease in size. The two longest removals show only a slight increase. At eighteen days the regenerated lengths are respectively 1.0, 1.2, 1.5, 2.6, 4.8 and 7.0 mm. as given in Table 38. The same data are represented in graphic form in Figure 14. Dividing by the removed lengths the fractions obtained are

$$\frac{1.0}{1.5}, \quad \frac{1.2}{2.8}, \quad \frac{1.5}{4.9}, \quad \frac{2.6}{8.4}, \quad \frac{4.8}{13.1}, \quad \text{and} \quad \frac{7.0}{18.1}$$

giving specific lengths of 0.67, 0.43, 0.31, 0.31, 0.37 and 0.39. The graph is shown in Figure 15.

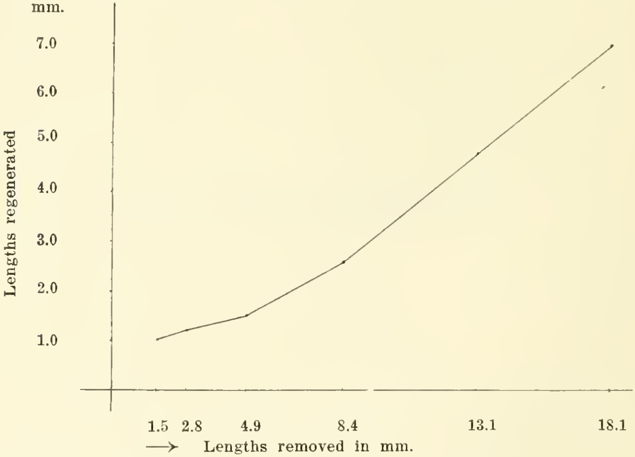

Figure 14 *Rana clamitans* Second regenerations Eighteen days

At eighteen days there is very little regeneration at any of the levels and at some of them, especially the shorter removals, a considerable absorption of regenerated material. Regeneration may therefore be considered as completed at this time. However the measurements for 56 days are given in order to show the changes. The regenerated lengths at that time are 0.9, 0.7, 1.6, 2.5, 5.2 and 7.1 mm. These data

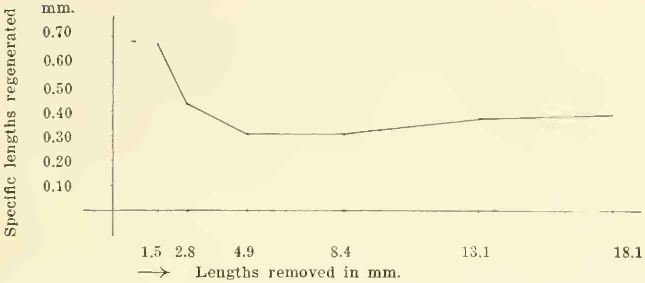

Figure 15 *Rana clamitans* Second regenerations Specific lengths Eighteen days

are given in table 38 and are represented in graphic form in figure 16. Dividing by the average removed lengths, which differ somewhat from the previous ones because of the death of certain individuals, the fractions obtained are

$$\frac{0.9}{1.5}, \quad \frac{0.7}{2.6}, \quad \frac{1.6}{4.9}, \quad \frac{2.5}{8.2}, \quad \frac{5.2}{13.2} \quad \text{and} \quad \frac{7.1}{17.9}$$

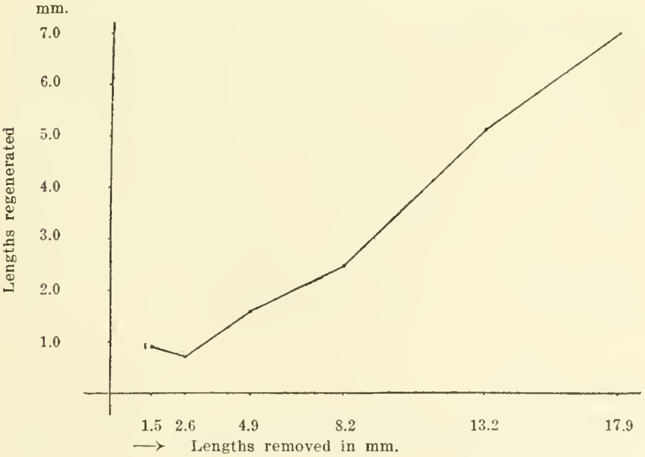

Figure 16 *Rana clamitans* Second regenerations Fifty-six days

giving specific regenerations of 0.60, 0.27, 0.33, 0.31, 0.39 and 0.40. These are shown in the graph given in figure 17. Because of the absorption of regenerated tissue in the shorter removals and a slight growth in the longer ones the latter show a comparative increase in specific lengths.

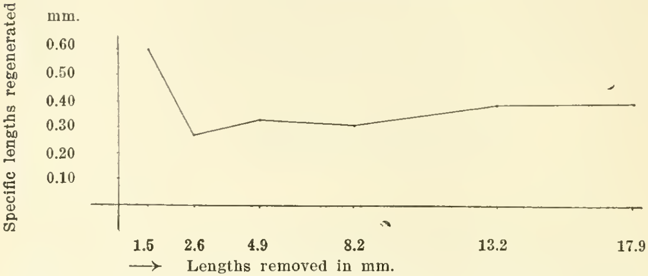

Figure 17 *Rana clamitans* Second regenerations Specific lengths Fifty-six days

For a comparison of completeness of regeneration it is better to take the greatest lengths regenerated at each level rather than the amounts regenerated at any particular time because the shorter levels complete regeneration and begin to absorb the tissues sooner than do the longer ones. On this basis the greatest regenerated lengths at each of the six levels are, for the 1.5 mm. level 1.0 mm. reached at ten days, for the 2.8 level 1.3 mm. reached at ten days, for the 4.9 level 1.6 mm. reached at twelve and a half days, for the 8.4 level 2.6 mm. reached at twelve and a half days, for the 13.2 level 5.2 mm. reached at fifty-six days, and for the 17.9 level 7.1 mm. reached at fifty-six days. These data are given in tables 37, 38, 39 and 40 and in graphic form in figure 18. At the last two levels there was a slight increase from eighteen to fifty-six days but this almost certainly came during the early part of the period and the values are therefore completed values. Dividing by the removed lengths the fractions obtained are

$$\frac{1.0}{1.5}, \quad \frac{1.3}{2.8}, \quad \frac{1.6}{4.9}, \quad \frac{2.6}{8.4}, \quad \frac{5.2}{13.2} \quad \text{and} \quad \frac{7.1}{17.9}$$

giving specific lengths of 0.67, 0.46, 0.33, 0.31, 0.39 and 0.40. The graph is given in Figure 19. The high values for the two short levels are probably due to the fact that the cells migrating to the cut surface form

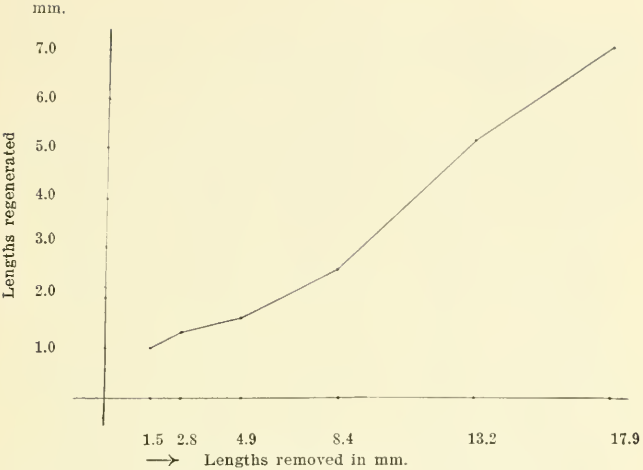

Figure 18 *Rana clamitans* Second regenerations Completeness

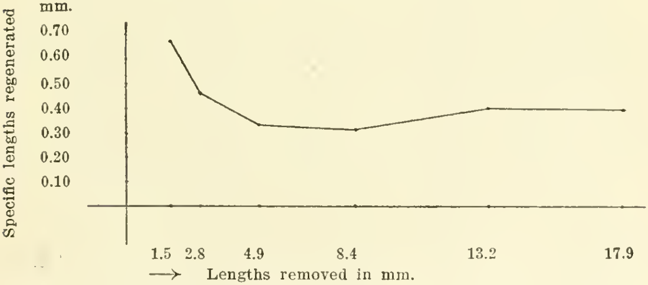

Figure 19 *Rana clamitans* Second regenerations Specific lengths Completeness

a large proportion of the total mass of the regenerated organ. Since apparently the length of this mass of cells is very much alike at all levels as indicated by the facts of the four day regenerations, the specific lengths for these short removals are greater than for the others. The high values of the two longest removals are due to a continuation of regeneration at these levels after it has ceased at the others. At ten days the specific lengths regenerated are very nearly the same at all the levels except the first two.

TABLE 37

Rana clamitans Series 3676-3765 Second regenerations

Percent removed Average	Catalog number	Removed length in mm.	4 Days		6 Days		8 Days		10 Days	
			Regenerated length mm.	Specific length	Regenerated length mm.	Specific length	Regenerated length mm.	Specific length	Regenerated length mm.	Specific length
6	3676	1.3	0.27		0.60		0.9		1.0	
	3682	1.6	0.18		0.60		0.9		1.0	
	3730	1.6	0.39		0.75		0.9		0.9	
	3754	1.6	0.06		0.55		0.9		1.1	
	Average	1.5	0.22	0.15	0.62	0.42	0.9	0.60	1.0	0.67
10	3677	2.0	0.30		0.6		0.9		0.9	
	3696	2.1	0.48		0.8		1.0		1.1	
	3701	3.2	0.42		0.8		1.1		1.2	
	3713	2.8	0.36		0.8		0.9		0.9	
	3719	3.1	0.30		0.8		1.1		1.4	
	3749	2.8	0.48		0.6		1.2		1.4	
	3750	3.5	0.42		1.3		1.7		1.9	
	Average	2.8	0.39	0.14	0.80	0.30	1.1	0.39	1.3	0.46
18	3678	5.0	0.20		0.5		0.9		1.0	
	3684	5.5	0.15		0.7		1.2		1.4	
	3702	4.7	0.42		0.8		1.1		1.3	
	3720	4.6	0.06		0.3		1.3		1.8	
	3756	4.8	0.36		1.0		1.3		1.7	
	Average	4.9	0.24	0.05	0.70	0.14	1.2	0.24	1.4	0.29

TABLE 37 (Continued)

Rana clamitans Series 3676-3765 Second regenerations

			4 Days		6 Days		8 Days		10 Days	
Percent removed Average	Catalog number	Removed length in mm.	Regenerated length mm.	Specific length	Regenerated length mm.	Specific length	Regenerated length mm.	Specific length	Regenerated length mm.	Specific length
31	3679	8.4	0.30		0.7		1.4		1.9	
	3685	9.3	0.60		1.2		1.9		2.3	
	3697	7.3	0.48		1.2		1.7		2.2	
	3703	9.3	0.45		1.3		2.0		2.5	
	3715	7.9	0.24		0.9		1.7		2.3	
	3721	8.7	0.57		1.3		1.9		2.3	
	3733	8.5	0.36		1.0		1.9		2.4	
	3739	9.6	0.36		1.0		1.8		2.4	
	3751	6.7	0.45		1.1		1.7		2.1	
	3757	8.0	0.42		1.2		2.1		2.8	
	Average	8.4	0.42	0.05	1.1	0.13	1.8	0.22	2.3	0.28
49	3686	14.5	0.60		2.1		3.4		4.8	
	3698	14.9	0.50		1.5		3.3		4.3	
	3704	14.5	0.45		2.2		3.3		4.4	
	3716	12.7	0.39		1.7		2.4		3.4	
	3722	12.5	0.60		1.6		2.6		3.6	
	3740	13.9	0.30		1.1		2.1		3.0	
	3752	11.2	0.54		1.7		2.5		3.4	
	3758	11.0	0.60		1.5		2.2		2.9	
	Average	13.1	0.50	0.04	1.7	0.13	2.7	0.21	3.7	0.28
67	3680	16.0	0.60		1.9		3.0		4.2	
	3681	21.2	0.84		3.0		4.0		5.6	
	3687	19.7	0.54		3.6		5.6		6.0	
	3699	21.0	0.54		2.2		4.3		5.9	
	3705	17.6	0.72		2.0		3.6		4.8	
	3717	17.6	0.42		2.6		3.6		5.2	
	3723	18.4	0.30		2.3		3.7		5.3	
	3735	16.5	0.48		2.0		3.4		5.5	
	3741	16.0	0.30		1.9		3.0		5.4	
	3753	16.8	0.42		2.0		2.5		3.8	
	Average	18.1	0.52	0.03	2.3	0.13	3.7	0.20	5.1	0.28

TABLE 38

Rana clamitans Series 3676-3765 Second regenerations

Percent removed Average	Catalog number	Removed length in mm.	12½ Days		18 Days		56 Days		Highest values	
			Regenerated length mm.	Specific length	Regenerated length mm.	Specific length	Regenerated length mm.	Specific length	Regenerated length mm.	Specific length
6	3676	1.3	1.0		1.0		0.7		1.0	
	3682	1.6	1.0		1.0		1.1		1.1	
	3730	1.6	0.9		0.9		0.7		0.9	
	3754	1.6	1.2		1.2		1.1		1.2	
	Average	**1.5**	**1.0**	**0.67**	**1.0**	**0.67**	**0.9**	**0.60**	**1.0**	**0.67**
10	3677	2.0	0.9		0.9		0.7		0.9	
	3696	2.1	1.0		1.0		0.7		1.1	
	3701	3.2	0.9		0.9		0.5		1.2	
	3713	2.8	1.4		1.3				1.4	
	3719	3.1	1.4		1.3		0.9		1.4	
	3749	2.8	2.0		2.0				2.0	
	3750	3.5	1.3		1.3				1.9	
	Average	**2.8**	**1.3**	**0.46**	**1.2**	**0.43**	**0.7**	**0.27**	**1.3**	**0.46**
18	3678	5.0	1.1		1.1				1.1	
	3684	5.5	1.4		1.5		1.4		1.5	
	3702	4.7	1.3		1.3		1.3		1.3	
	3720	4.6	2.3		1.9		2.0		2.3	
	3756	4.8	1.8		1.6				1.8	
	Average	**4.9**	**1.6**	**0.33**	**1.5**	**0.31**	**1.6**	**0.33**	**1.6**	**0.33**
31	3679	8.4	1.9		2.1				2.1	
	3685	9.3	2.8		3.0		2.6		3.0	
	3697	7.3	2.4		2.3		2.1		2.4	
	3703	9.3	2.6		2.5		2.5		2.5	
	3715	7.9	2.6		2.6		2.8		2.8	
	3721	8.7	2.6		2.3		2.2		2.6	
	3733	8.5	2.6		2.6		2.8		2.8	
	3739	9.6	3.0		2.9				3.0	
	3751	6.7	2.4		2.5		2.3		2.5	
	3757	8.0	3.1		3.2		3.1		3.2	
	Average	**8.4**	**2.6**	**0.31**	**2.6**	**0.31**	**2.5**	**0.31**	**2.6**	**0.31**

TABLE 38 (Continued)

Percent removed Average	Catalog number	Removed length in mm.	12½ Days		18 Days		56 Days		Highest values	
			Regenerated length mm.	Specific length	Regenerated length mm.	Specific length	Regenerated length mm.	Specific length	Regenerated length mm.	Specific length
49	3686	14.5	5.3		5.2				5.3	
	3698	14.9	5.0		5.4		5.4		5.4	
	3704	14.5	5.2		5.5		5.4		5.5	
	3716	12.7	4.2		5.1		4.4		5.1	
	3722	12.5	3.9		3.5		4.2		4.2	
	3740	13.9	4.6		5.6		6.8		6.8	
	3752	11.2	4.1		4.0				4.1	
	3758	11.0	3.6		4.1		4.9		4.9	
	Average	13.1	4.4	0.34	4.8	0.37	5.2	0.39	5.2	0.39
67	3680	16.0	5.2		6.4		6.6		6.6	
	3681	21.2	6.3		7.3		7.2		7.3	
	3687	19.7	6.6		7.0				7.0	
	3699	21.0	7.1		7.5		7.2		7.5	
	3705	17.6	6.4		6.2		6.0		6.4	
	3717	17.6	6.0		6.7		6.4		6.7	
	3723	18.4	6.5		8.1		8.3		8.3	
	3735	16.5	6.5		7.8		8.0		8.0	
	3741	16.0	5.8		6.9		7.0		7.0	
	3753	16.8	5.2		6.4		7.1		7.1	
	Average	18.1	6.2	0.34	7.0	0.39	7.1	0.40	7.1	0.40

TABLE 39

Rana clamitans Series 3676-3765 Summary Second regenerations

Lengths regenerated at different levels at different times

Percent of tail length removed	Length removed in mm.	Number of individuals	Days after operation						
			4	6	8	10	12½	18	56
6	1.5	4	0.22	0.6	0.9	1.0	1.0	1.0	0.9
10	2.8	7	0.39	0.8	1.1	1.3	1.3	1.2	0.7
18	4.9	5	0.24	0.7	1.2	1.4	1.6	1.5	1.6
31	8.4	10	0.42	1.1	1.8	2.3	2.6	2.6	2.5
49	13.1	8	0.50	1.7	2.7	3.7	4.4	4.8	5.2
67	18.1	10	0.52	2.3	3.7	5.1	6.2	7.0	7.1

TABLE 40

Rana clamitans .Series 3676-3765 Summary Second regenerations
Lengths regenerated at different levels at different times

Percent of tail length removed	Length removed in mm.	Number of individuals	Days after operation						
			4	6	8	10	12½	18	56
6	1.5	4	0.15	0.42	0.60	0.67	0.67	0.67	0.60
10	2.8	7	0.14	0.30	0.39	0.46	0.46	0.43	0.27
18	4.9	5	0.05	0.14	0.24	0.29	0.33	0.31	0.33
31	8.4	10	0.05	0.13	0.22	0.28	0.31	0.31	0.31
49	13.1	8	0.04	0.13	0.21	0.28	0.34	0.37	0.39
67	18.1	10	0.03	0.13	0.20	0.28	0.34	0.39	0.40

First Regenerations

The data for first regenerations are from a different set of individuals than those for second regenerations. The two kinds of operations were made on the same day. The general results obtained from the first regenerations are in full agreement with those obtained from the second regenerations but there is greater variability because of the smaller number of individuals. The average per cents of the tail length removed are respectively 6, 10, 17, 30, 48 and 62 for the six levels. The first of these has two individuals averaging 1.5 mm. of removed tail, the second five individuals with an average of 2.6 mm., the third three individuals with an average of 4.6, the fourth eight with an average of 8.2, the fifth five with an average of 13.0 and the sixth five with an average of 16.7. The data for these experiments are given in Tables 41, 42, 43 and 44 and in Figures 20 to 35.

The progress of a first regeneration is similar to that of a second except that the maximum is reached later in the case of first regenerations. In the present series the maximum specific rate for first regenerations comes between the sixth and the eighth day after the operation. A comparison of the two regenerations is made in the section on the effect of successive removal. The change in rate during the process of regeneration is also discussed in a separate section.

The lengths regenerated during the first four days are respectively 0.27, 0.15, 0.51, 0.45, 0.46 and 0.51 for the six levels. There is no regular increase with removed length. The data are given in Table 41 and in Figure 20. The specific lengths regenerated are 0.17, 0.06, 0.11, 0.05, 0.03 and 0.03. They are shown in Table 41 and in Figure 21. As in the case of the second regeneration the shortest removals have the largest proportional amounts. This first period being the period of cell migration with very little cell division it is probable that the length of the material furnished in this way, as measured along the main axis of the individual, is independent of the level of the cut. The area of the cut surface of course is greater at the more proximal than at the more distal levels so that the actual total mass of regenerated material is greater at the deeper levels.

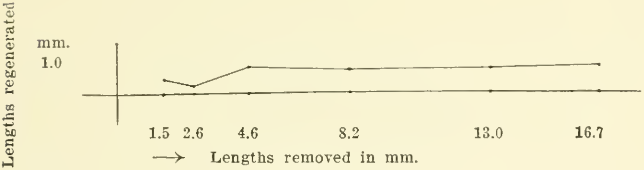

Figure 20 *Rana clamitans* First regenerations Four days

At six days the rate of first regenerations is rapidly increasing, the maximum rate coming between six and eight days. The lengths regenerated at six days are respectively 0.47, 0.5, 1.0, 1.1, 1.6 and 1.6 mm.

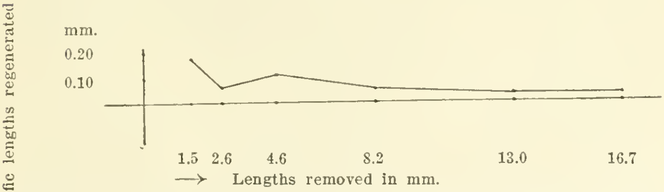

Figure 21 *Rana clamitans* First regenerations Specific lengths Four days

They are shown in Table 41 and in Figure 22. There is in general an increase with increase in removed length but the first is not proportional to the second. The specific lengths are 0.30, 0.18, 0.22, 0.13, 0.12 and 0.09 as shown in Table 41 and Figure 23. The shorter removals still have proportionately the greater regenerations.

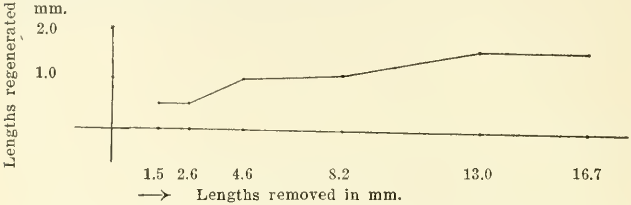

Figure 22 *Rana clamitans.* First regenerations Six days

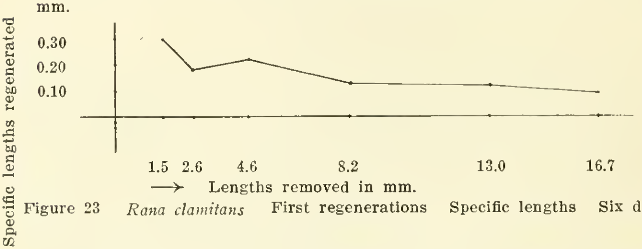

Figure 23 *Rana clamitans* First regenerations Specific lengths Six days

The maximum rate of regeneration is reached between the sixth and the eighth day. The regenerated lengths at eight days are 0.8, 0.7, 1.5, 1.7, 2.6 and 3.0 mm. The data are shown in Table 41 and Figure 24. With one exception there is increase in regenerated length with increase in removed length. The specific regenerated lengths are 0.53, 0.27, 0.33, 0.21, 0.20 and 0.18 as shown in Table 41 and Figure 25. The shortest removals have the greatest specific regenerations but at 8.2 mm. and above there is an approach to constancy.

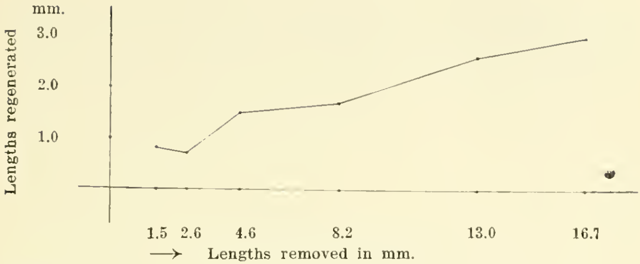

Figure 24 *Rana clamitans* First regenerations Eight days

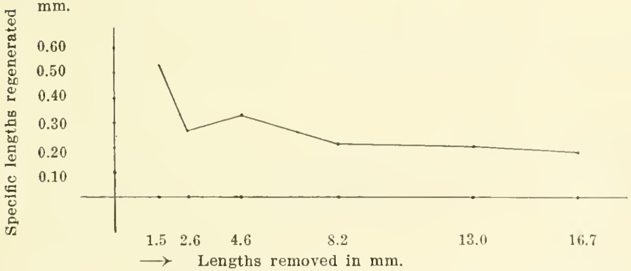

Figure 25 *Rana clamitans* First regenerations Specific lengths Eight days

Between the eighth and the tenth day there is a rapid decrease in rate associated with tissue differentiation. The regenerated lengths at ten days are 0.9, 1.0, 1.7, 2.3, 3.8 and 4.5 mm. as shown in Table 41 and Figure 26. There is an uninterrupted increase in regeneration with increase in removed length. The specific lengths are 0.58, 0.38, 0.37, 0.28, 0.29 and 0.27 as shown in Table 41 and Figure 27.

Between ten and twelve and a half days regeneration is slow, reaching its end for the two shortest removals at the latter day. The regenerated lengths at twelve and a half days are 0.9, 1.2, 1.8, 2.6, 4.7 and 5.8 mm. as shown in Table 42 and Figure 28. There is a steady increase with increase in removed length. The specific lengths are 0.61, 0.46, 0.39, 0.31, 0.36 and 0.35 as shown in Table 42 and Figure 29. There is an approach to constancy in the four largest removals.

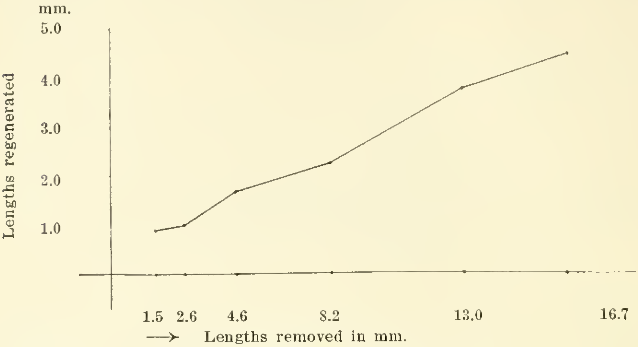

Figure 26 *Rana clamitans.* First regenerations Ten days

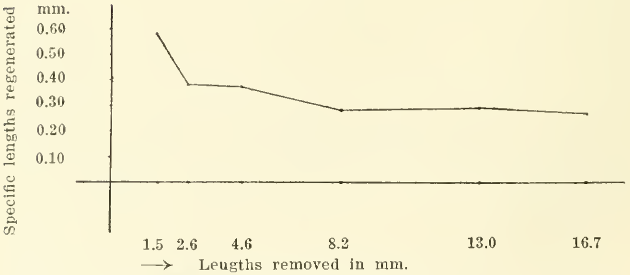

Figure 27 *Rana clamitans* First regenerations Specific lengths Ten days

Between twelve and a half and eighteen days the regenerated material is decreasing in the case of the two shortest removals, has made no progress in the third and in the three longest removals the increase is very slight. The data therefore are of value more particularly in connection with the problem of the relative completeness of regeneration from the different levels. The regenerated lengths at eighteen days are

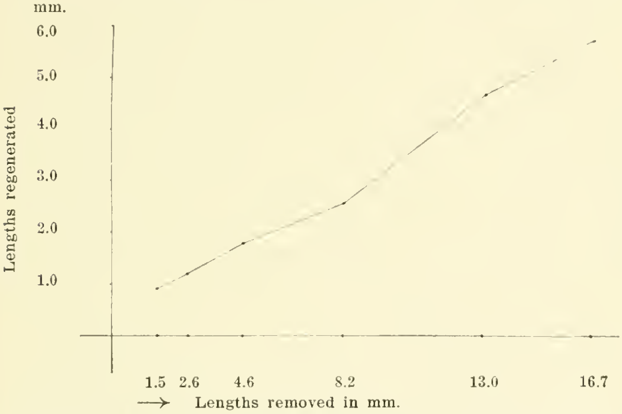

Figure 28 *Rana clamitans* First regenerations Twelve and a half days

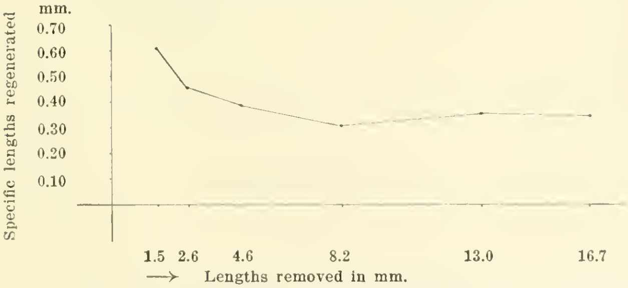

Figure 29 *Rana clamitans* First regenerations Specific lengths Twelve and a half days

0.9, 1.1, 1.8, 2.7, 5.5 and 6.8 mm. as shown in Table 42 and Figure 30. There is a regular increase with increase in removed length. The specific lengths are 0.60, 0.42, 0.39, 0.33, 0.42 and 0.40 as shown in Table 42 and Figure 31. Though there are irregularities the specific lengths approach constancy at all levels except the most distal one.

Between eighteen and fifty-six days there is practically no increase

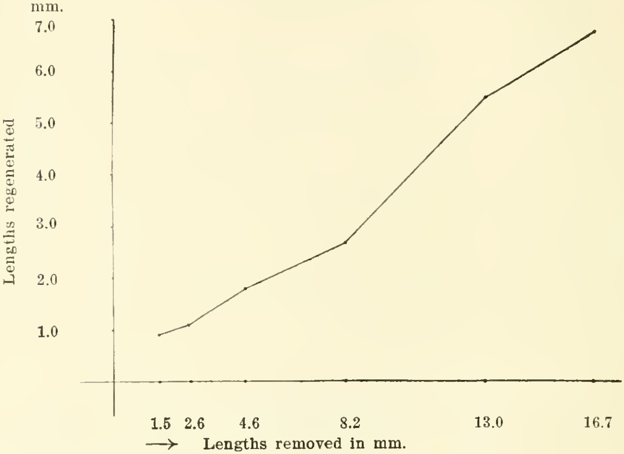

Figure 30 *Rana clamitans.* First regenerations Eighteen days

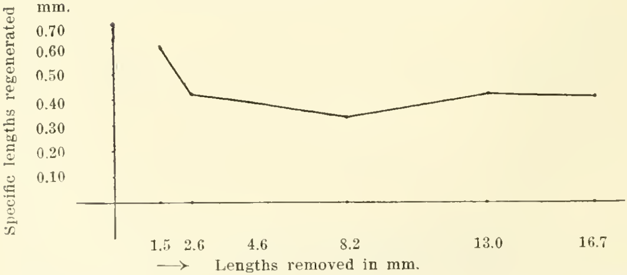

Figure 31 *Rana clamitans* First regenerations Specific lengths Eighteen days

in regenerated length and some absorption of material especially with the shorter removals. The regenerated lengths at fifty-six days are 0.7, 1.1, 1.5, 2.5, 5.5 and 6.9 mm. as shown in Table 42 and Figure 32. There is a regular increase in regeneration from the shortest to the longest removal. The specific lengths are 0.45, 0.42, 0.34, 0.30, 0.42 and 0.41 as shown in Table 42 and Figure 33. These data are of value only for

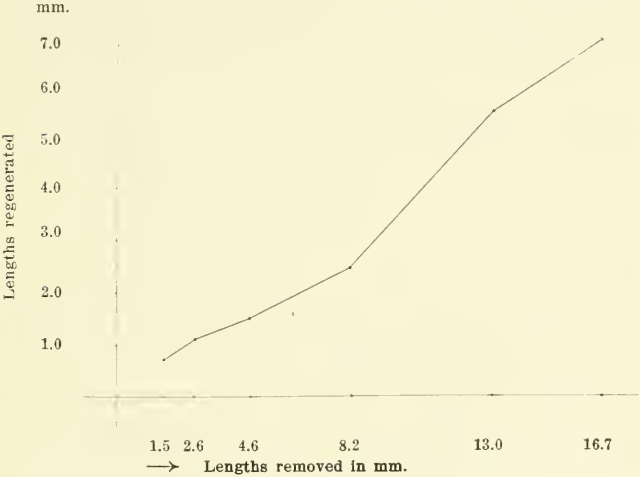

Figure 32 *Rana clamitans* First regenerations Fifty-six days

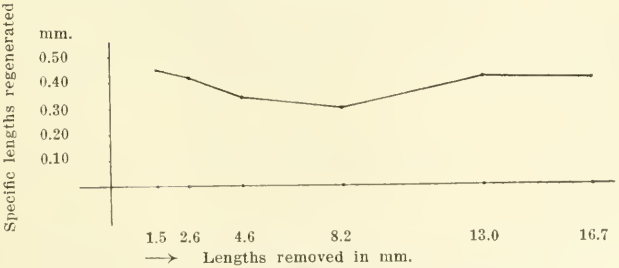

Figure 33 *Rana clamitans* First regenerations Specific lengths Fifty-six days

a comparison of completeness of regeneration but for such a comparison it is better in some ways to compare the regenerations at the time when absorption has not begun. The greatest average regenerated length attained for the 1.5 mm. level is 0.9 mm. at ten days, for the 2.6 level 1.2 at twelve and a half days, for the 4.6 level 1.8 at twelve and a half days, for the 8.2 level 2.7 at eighteen days, for the 13.0 level 5.5 at eighteen days and for the 16.7 level 6.9 at fifty-six days. There is an uninterrupted increase from the shortest to the longest removal in complete amount regenerated. This is shown graphically in Figure 34. The

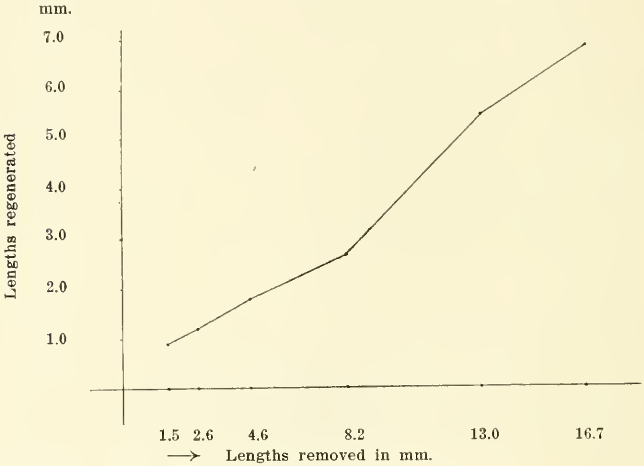

Figure 34 *Rana clamitans* First regenerations Completeness

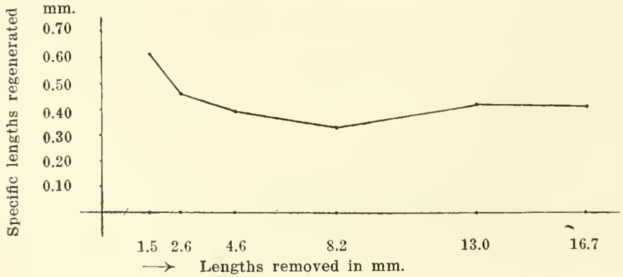

Figure 35 *Rana clamitans* First regenerations Specific lengths Completeness

completed regenerations are less than the removed lengths. The specific completed regenerated lengths obtained as before by dividing by the removed lengths are 0.61, 0.46, 0.39, 0.33, 0.42 and 0.41, as shown in table 42 and figure 35. The greater specific lengths from the shortest removals are probably due as in the case of the second regenerations to the fact that a greater proportion of their substance is made up of cells that have migrated over the cut surface during the first stages of regeneration. This migrated material is not essentially different in axial length at the different levels. The largest removals have a greater specific length than the medium ones because regeneration continues at the former levels after it has ceased at the latter.

On the whole there is no essential difference between the results obtained from first regenerations and those obtained from second regenerations. The latter give the more regular data because the averages are taken from a larger number of individuals.

TABLE 41

Rana clamitans Series 3676-3765 First regenerations

Percent removed Average	Catalog number	Removed length in mm.	4 Days		6 Days		8 Days		10 Days	
			Regenerated length mm.	Specific length	Regenerated length mm.	Specific length	Regenerated length mm.	Specific length	Regenerated length mm.	Specific length
6	3706	1.4	0.24		0.54		0.9		1.0	
	3742	1.7	0.30		0.40		0.7		0.8	
	Average	1.5	0.27	0.17	0.47	0.30	0.8	0.53	0.9	0.58
10	3688	2.5	0.12		0.3		0.3		0.7	
	3707	3.2	0.24		0.8		1.1		1.4	
	3724	2.6	0.06		0.5		0.8		1.1	
	3743	2.5	0.03		0.1		0.4		0.8	
	3760	3.1	0.30		0.6		0.9		1.1	
	Average	2.6	0.15	0.06	0.5	0.18	0.7	0.27	1.0	0.38

TABLE 41 (Continued)

Percent removed Average	Catalog number	Removed length in mm.	4 Days		6 Days		8 Days		10 Days	
			Regenerated length mm.	Specific length	Regenerated length mm.	Specific length	Regenerated length mm.	Specific length	Regenerated length mm.	Specific length
17	3708	5.3	0.54		1.2		1.9		2.1	
	3726	4.3	0.42		0.9		1.3		1.4	
	3762	4.1	0.57		1.0		1.2		1.5	
	Average	**4.6**	**0.51**	**0.11**	**1.0**	**0.22**	**1.5**	**0.33**	**1.7**	**0.37**
30	3690	9.7	0.48		1.0		1.7		2.4	
	3709	8.8	0.48		1.3		2.0		2.6	
	3727	8.3	0.48		1.1		1.6		2.0	
	3745	10.0	0.54		1.8		2.4		3.8	
	3744	6.0	0.36		1.0		1.3		1.7	
	3761	6.6	0.39		1.0		1.5		1.9	
	3763	8.5	0.57		1.1		1.8		2.4	
	3689	6.3	0.30		0.7		1.2		1.5	
	Average	**8.2**	**0.45**	**0.05**	**1.1**	**0.13**	**1.7**	**0.21**	**2.3**	**0.28**
48	3710	12.3	0.42		1.8		2.9		3.7	
	3728	12.8	0.60		1.7		2.8		3.9	
	3746	13.3	0.54		1.7		2.4		4.1	
	3764	14.6	0.42		1.3		2.5		4.2	
	3765	12.2	0.30		1.5		2.3		3.2	
	Average	**13.0**	**0.46**	**0.03**	**1.6**	**0.12**	**2.6**	**0.20**	**3.8**	**0.29**
62	3692	16.8	0.51		1.1		2.2		3.2	
	3693	17.2	0.48		1.8		3.3		5.0	
	3711	17.0	0.54		1.8		3.6		5.6	
	3729	16.1	0.48		1.9		3.3		4.6	
	3749	16.2	0.54		1.2		2.7		4.2	
	Average	**16.7**	**0.51**	**0.03**	**1.6**	**0.09**	**3.0**	**0.18**	**4.5**	**0.27**

TABLE 42

Rana clamitans Series 3676-3765 First regenerations

Percent removed Average	Catalog number	Removed length in mm.	12½ Days		18 Days		56 Days	
			Regenerated length mm.	Specific length	Regenerated length mm.	Specific length	Regenerated length mm.	Specific length
6	3706	1.4	1.0		0.9		0.7	
	3742	1.7	0.9		0.9		0.7	
	Average	**1.5**	**0.9**	**0.61**	**0.9**	**0.60**	**0.7**	**0.45**
10	3688	2.5	0.9		0.9		0.7	
	3707	3.2	1.4		1.3		0.7	
	3724	2.6	1.4		1.4		1.2	
	3743	2.5	1.0		1.0		1.7	
	3760	3.1	1.2		1.1		1.1	
	Average	**2.6**	**1.2**	**0.46**	**1.1**	**0.42**	**1.1**	**0.42**
17	3708	5.3	2.3		2.3		1.8	
	3726	4.3	1.4		1.4		1.4	
	3762	4.1	1.7		1.8		1.4	
	Average	**4.6**	**1.8**	**0.39**	**1.8**	**0.39**	**1.5**	**0.34**
30	3690	9.7	2.6		2.7		2.2	
	3709	8.8	3.2		3.4		3.3	
	3727	8.3	2.2		2.2		2.2	
	3745	10.0	4.4		4.8		4.2	
	3744	6.0	1.8		1.7			
	3761	6.6	2.2		2.3		1.8	
	3763	8.5	2.9		3.1			
	3689	6.3	1.6		1.7		1.4	
	Average	**8.2**	**2.6**	**0.31**	**2.7**	**0.33**	**2.5**	**0.30**
48	3710	12.3	3.9		3.9		3.9	
	3728	12.8	4.8		5.4		5.8	
	3746	13.3	5.7		7.0		6.8	
	3764	14.6	5.3		6.8		6.5	
	3765	12.2	3.9		4.5		4.5	
	Average	**13.0**	**4.7**	**0.36**	**5.5**	**0.42**	**5.5**	**0.42**
62	3692	16.8	4.3		5.0		5.2	
	3693	17.2	6.5		7.3		6.6	
	3711	17.0	7.0		7.7		8.3	
	3729	16.1	5.5		6.7		6.4	
	3749	16.2	5.6		7.1		7.8	
	Average	**16.7**	**5.8**	**0.35**	**6.8**	**0.40**	**6.9**	**0.41**

TABLE 43

Rana clamitans Series 3676-3765 Summary First regenerations
Lengths regenerated at different levels at different times

Percent of tail length removed	Length removed in mm.	Number of individuals	Days after operation						
			4	6	8	10	12½	18	56
6	1.5	2	0.27	0.5	0.8	0.9	0.9	0.9	0.7
10	2.6	5	0.15	0.5	0.7	1.0	1.2	1.1	1.1
17	4.6	3	0.51	1.0	1.5	1.7	1.8	1.8	1.5
30	8.2	8	0.45	1.1	1.7	2.3	2.6	2.7	2.5
48	13.0	5	0.46	1.6	2.6	3.8	4.7	5.5	5.5
62	16.7	5	0.51	1.6	3.0	4.5	5.8	6.8	6.9

TABLE 44

Rana clamitans Series 3676-3765 Summary First regenerations
Specific lengths regenerated at different levels at different times

Percent of tail length removed	Length removed in mm.	Number of individuals	Days after operation						
			4	6	8	10	12½	18	56
6	1.5	2	0.17	0.30	0.53	0.58	0.61	0.60	0.45
10	2.6	5	0.06	0.18	0.27	0.38	0.46	0.42	0.42
17	4.6	3	0.11	0.22	0.33	0.37	0.39	0.39	0.34
30	8.2	8	0.05	0.13	0.21	0.28	0.31	0.33	0.30
48	13.0	5	0.03	0.12	0.20	0.29	0.36	0.42	0.42
62	16.7	5	0.03	0.09	0.18	0.27	0.35	0.40	0.41

EXPERIMENT II AMBLYSTOMA PUNCTATUM SERIES 4600-5052

The eggs were hatched on March 29 to April 4, 1913. Operations on the tail were made on May 7 in numbers 4600-4752 and on May 10 in numbers 4800-5052. The removed lengths were approximately $^{1}/_{10}$, $^{1}/_{5}$, $^{1}/_{3}$, $^{1}/_{2}$ and $^{3}/_{4}$ of the tail length. Measurements of the regenerated tissue were made at 2, 4, 6, 8-9, 10-11, 13, 15-16 and 17-18 days after the operation. The data are given in Tables 45 to 54 and in Figures 36 to 51.

The salamander larvae are much more irregular in their regeneration as well as in ordinary growth than frog tadpoles. The measurements in the present experiment were made on killed individuals so that only a single regeneration measurement is made in a single individual. This procedure also tends toward a greater variability in the data. The number of individuals in any particular measurement also is less than for the second regeneration of frog tadpoles.

Notwithstanding all these unwelcome factors the general features of regeneration are similar to those for the tadpole experiment. The regenerated length at any time is approximately proportional to the removed length. It is true even in the earliest measurements. As for frog tadpoles the shorter removals have proportionately a larger regeneration than the others at practically each time of measurement. The approach to equality in specific lengths is true only of the lengths of removal equal to one-fifth or more of the tail length.

At two days the regenerated lengths are respectively 0.10, 0.15, 0.15, 0.47 and 0.53 mm. for the five levels of removal. They give specific lengths of 0.07, 0.07, 0.04, 0.08 and 0.06 as shown Table 45 and Figures 36 and 37.

At four days the regenerated lengths are 0.12, 0.15, 0.30, 0.41 and 0.40 mm. and the specific lengths 0.11, 0.07, 0.07, 0.07 and 0.05 as shown in Table 46 and Figures 38 and 39.

At six days the regenerated lengths are 0.32, 0.47, 0.62, 0.70 and 1.02 mm. and the specific lengths 0.30, 0.20, 0.16, 0.12 and 0.11 as shown in Table 47 and Figures 40 and 41.

At eight to nine days the regenerated lengths are 0.40, 0.65, 0.80, 1.40 and 1.52 mm. and the specific lengths 0.44, 0.28, 0.23, 0.23 and 0.19 as shown in Table 48 and Figures 42 and 43.

At ten to eleven days the regenerated lengths are 0.50, 0.63, 1.54, 2.22 and 2.22 mm. and the specific lengths 0.62, 0.26, 0.43, 0.41 and 0.27 as shown in Table 49 and Figures 44 and 45.

At thirteen days the regenerated lengths are 0.78, 0.92, 1.74, 2.40 and 3.60 mm and the specific lengths 0.74, 0.43, 0.48, 0.44 and 0.48 as shown in Table 50 and Figures 46 and 47.

At fifteen to sixteen days the regenerated lengths are 0.80, 1.30, 1.37, 2.80 and 3.80 mm. and the specific lengths 0.67, 0.61, 0.40, 0.48 and 0.54 as shown in Table 51 and Figures 48 and 49.

At seventeen to eighteen days the regenerated lengths are 0.70, 1.40, 1.60, 3.80 and 4.67 mm. and the specific lengths 0.67, 0.62, 0.41, 0.66 and 0.57 as shown in Table 52 and Figures 50 and 51.

A summary of regenerated lengths is given in Table 53 and of specific regenerated lengths in Table 54.

Since the experiment was closed at eighteen days and since the measurements at different times were made on different individuals it is not possible to make as accurate a comparison of completeness of regeneration as in the case of the frog tadpoles. For the three shortest removals regeneration is probably completed at this time but this is not true for the two longest ones. In this respect as in others there is an agreement with the former experiment. The percent of the removed tail that is regenerated is greater for all levels than in the frog tadpoles. It is probable also that if the longest removals had been allowed to complete their regenerations their specific regenerations as in the case of the frog tadpoles would have been shown to be greater than those for medium levels.

TABLE 45

Amblystoma punctatum. Series 4600-5052. Average tail length =10.9 mm.
Regeneration: 2 days

Percent of tail length removed Average	Catalog number	Removed length mm.	Regenerated length mm.	Specific length regenerated
14	5022	1.5	0.1	
	Average .	**1.5**	**0.10**	**0.07**
20	4641	2.3	0.2	
	4741	1.9	0.1	
	4841	2.2	0.1	
	5050b	2.3	0.2	
	Average	**2.2**	**0.15**	**0.07**
32	4811	3.9	0.3	
	4911	3.3	0.1	
	5012	3.3	0.05	
	Average	**3.5**	**0.15**	**0.04**
53	4601	6.0	0.3	
	4801	6.0	0.7	
	5001	5.4	0.4	
	Average	**5.8**	**0.47**	**0.08**
81	4631	9.5	0.7	
	4831	9.1	0.6	
	5032	7.9	0.3	
	Average	**8.8**	**0.53**	**0.06**

The data from both experiments show that except for very short removals the length regenerated in a given time is approximately proportional to the length removed.

TABLE 46

Amblystoma punctatum. Series 4600-5052. Average tail length=10.9 mm. Regeneration: 4 days

Percent of tail length removed Average	Catalog number	Removed length mm.	Regenerated length mm.	Specific length regenerated
10	4622	0.9	0.1	
	4722	0.8	0.2	
	4822	1.5	0.1	
	4922	0.8	0.1	
	5024	1.6	0.1	
	Average	1.1	0.12	0.11
21	4742	2.4	0.1	
	4842	2.3	0.2	
	Average	2.3	0.15	0.07
37	4612	3.7	0.3	
	4712	3.6	0.2	
	4812	4.5	0.4	
	5012	4.2	0.3	
	Average	4.0	0.30	0.07
55	4602	6.0	0.2	
	4702	6.0	0.05	
	4802	6.2	0.7	
	4902	6.0	0.5	
	5004	5.9	0.6	
	Average	6.0	0.41	0.07
76	4632	9.3	0.4	
	4732	8.5	0.2	
	4832	10.9	0.6	
	4932	5.9	0.4	
	5034	7.1	0.4	
	Average	8.3	0.40	0.05

TABLE 47

Amblystoma punctatum. Series 4600-5052. Average tail length=10.9 mm.
Regeneration: 6 days

Percent of tail length removed Average	Catalog number	Removed length mm.	Regenerated length mm.	Specific length regenerated
10	4623	1.0	0.3	
	4723	0.8	0.2	
	4923	1.6	0.6	
	——	1.1	0.2	
	Average	**1.1**	**0.32**	**0.30**
21	4643	2.1	0.7	
	4743	2.2	0.2	
	4843	2.1	0.4	
	4943	2.8	0.6	
	Average	**2.3**	**0.47**	**0.20**
35	4613	3.6	0.6	
	4713	2.9	0.6	
	4820b	4.4	0.8	
	4913	4.5	0.6	
	5013	3.6	0.5	
	Average	**3.8**	**0.62**	**0.16**
54	4603	6.1	0.4	
	4703	6.7	0.4	
	4803	5.3	1.4	
	5003	5.6	0.6	
	Average	**5.9**	**0.70**	**0.12**
82	4633	8.8	0.6	
	4733	8.2	0.9	
	4833	10.6	1.8	
	5033	7.9	0.8	
	Average	**8.9**	**1.02**	**0.11**

TABLE 48

Amblystoma punctatum Series 4600-5052 Average tail length=10.9 mm. Regeneration: 8-9 days (8 for 4800-5052, 9 for 4600-4752)

Percent of tail length removed Average	Catalog number	Removed length mm.	Regenerated length mm.	Specific length regenerated
8	4724	0.7	0.2	
	4824	1.1	0.7	
	5026	1.0	0.3	
	Average	0.9	0.40	0.44
21	4644	2.3	0.6	
	4844	2.3	1.0	
	4944	2.2	0.7	
	5045	2.3	0.3	
	Average	2.3	0.65	0.28
31	4614	3.0	0.8	
	4624	3.0	0.4	
	4714	3.4	1.2	
	4814	3.7	1.0	
	4914	3.2	0.6	
	5016	4.3	0.8	
	Average	3.4	0.80	0.23
56	4604	6.0	1.8	
	4704	6.3	1.7	
	4804	5.9	1.4	
	4904	5.4	0.9	
	5006	6.8	1.2	
	Average	6.1	1.40	0.23
75	4634	8.3	2.1	
	4734	8.0	1.3	
	4834	9.0	1.6	
	4934	7.5	1.1	
	Average	8.2	1.52	0.19

TABLE 49

Amblystoma punctatum Series 4600-5052 Average tail length=10.9 mm.
Regeneration: 10-11 days (10 for 4800-5052, 11 for 4600-4752)

Percent of tail length removed Average	Catalog number	Removed length mm.	Regenerated length mm.	Specific length regenerated
7	4725	0.6	0.3	
	4825	0.8	0.6	
	5027	1.0	0.6	
	Average	0.8	0.50	0.62
23	4746	2.6	0.4	
	4845	2.6	1.0	
	5046	2.2	0.5	
	Average	2.5	0.63	0.26
33	4620b	3.0	1.9	
	4715	3.0	1.8	
	4815	4.3	2.0	
	4920	3.6	1.2	
	5017	3.9	0.8	
	Average	3.6	1.54	0.43
50	4605	5.2	2.8	
	4705	4.6	1.4	
	4805	6.3	2.8	
	4910b	5.0	1.9	
	5007	6.0	2.2	
	Average	5.4..	2.22	0.41
74	4735	7.5	2.5	
	4835	9.4	2.9	
	4935	7.6	1.3	
	5037	8.1	2.2	
	Average	8.1	2.22	0.27

TABLE 50

Amblystoma punctatum. Series 4600-5052. Average tail length=10.9 mm.
Regeneration: 13 days

Percent of tail length removed Average	Catalog number	Removed length mm.	Regenerated length mm.	Specific length regenerated
10	4626	1.4	0.8	
	4726	1.0	0.6	
	4830b	1.0	0.7	
	4926	1.0	0.9	
	5028	0.9	0.9	
	Average	1.1	0.78	0.74
19	4646	1.9	1.4	
	4745	2.2	0.8	
	4846	2.6	1.0	
	4946	1.9	0.5	
	Average	2.1	0.92	0.43
32	4616	3.6	1.8	
	4716	3.2	2.0	
	4816	3.9	2.5	
	4916	3.7	1.6	
	5018	3.7	0.8	
	Average	3.6	1.74	0.48
50	4706	6.4	2.3	
	4806	5.8	2.9	
	4910	5.0	2.5	
	5008	4.5	1.9	
	Average	5.4	2.40	0.44
69	4636	8.1	3.4	
	4740b	7.7	4.7	
	4936	7.4	3.5	
	5038	6.7	2.8	
	Average	7.5	3.60	0.48

TABLE 51

Amblystoma punctatum. Series 4600-5052. Average tail length=10.9 mm. Regeneration: 15-16 days (15 for 4800-5052, 16 for 4600-47g2)

Percent of tail length removed Average	Catalog number	Removed length mm.	Regenerated length mm.	Specific length regenerated
11	4927	1.2	0.8	
	5029	1.2	0.8	
	Average	**1.2**	**0.80**	**0.67**
19	4647	1.9	1.5	
	4747	2.7	1.7	
	4847	2.4	1.0	
	4950b	1.9	1.2	
	5049	1.8	1.1	
	Average	**2.1**	**1.30**	**0.61**
32	4617	3.1	1.4	
	4717	3.5	1.3	
	4917	3.2	1.8	
	5019	4.1	1.0	
	Average	**3.5**	**1.37**	**0.40**
53	4607	5.7	2.7	
	4807	5.7	2.9	
	4817	5.2	2.6	
	5009	6.6	3.0	
	Average	**5.8**	**2.80**	**0.48**
64	4937	7.0	3.8	
	Average	**7.0**	**3.80**	**0.54**

TABLE 52

Amblystoma punctatum. Series 4600-5052. Average tail length=10.9 mm. Regeneration: 17-18 days (18 for 4800-5052, 17 for 4600-4752)

Percent of tail length removed Average	Catalog number	Removed length mm.	Regenerated length mm.	Specific length regenerated
10	4828	1.0	0.8	
	4929	1.1	0.6	
	Average	**1.0**	**0.70**	**0.67**
20	4648	2.1	1.5	
	4749	2.6	2.1	
	4848	2.1	1.1	
	4949	2.2	1.3	
	5050	2.2	1.0	
	Average	**2.2**	**1.40**	**0.62**
36	4718	3.9	1.6	
	Average	**3.9**	**1.60**	**0.41**
53	4608	5.4	4.2	
	4708	6.6	4.1	
	4808	5.4	3.1	
	Average	**5.8**	**3.80**	**0.66**
76	4838	9.4	5.0	
	4939	6.4	4.5	
	5040	9.0	4.5	
	Average	**8.3**	**4.67**	**0.57**

TABLE 53

Amblystoma punctatum Series 4600-5052 Summary Regenerated lengths (Tables 45 to 52)

Percent of tail length removed Average	Length removed mm. Average	Average length regenerated in mm.							
		2 Days	4 Days	6 Days	8-9 Days	10-11 Days	13 Days	15-16 Days	17-18 Days
10	1.1	0.10	0.12	0.32	0.40	0.50	0.78	0.80	0.70
21	2.2	0.15	0.15	0.47	0.65	0.63	0.92	1.30	1.40
34	3.7	0.15	0.30	0.62	0.80	1.54	1.74	1.37	1.60
53	5.8	0.47	0.41	0.70	1.40	2.22	2.40	2.80	3.80
74	8.1	0.53	0.40	0.94	1.52	2.22	3.60	3.80	4.70

TABLE 54

Amblystoma punctatum Series 4600-5052 Summary Specific lengths regenerated (Tables 45 to 52)

Percent of tail length removed Average	Length removed mm. Average	Average specific regenerated lengths							
		2 Days	4 Days	6 Days	8-9 Days	10-11 Days	13 Days	15-16 Days	17-18 Days
10	1.1	0.07	0.11	0.30	0.43	0.62	0.74	0.67	0.67
21	2.2	0.07	0.06	0.20	0.28	0.26	0.43	0.61	0.62
34	3.7	0.04	0.07	0.16	0.23	0.43	0.48	0.40	0.41
53	5.8	0.08	0.07	0.12	0.23	0.41	0.44	0.48	0.66
74	8.1	0.06	0.15	0.11	0.19	0.27	0.48	0.54	0.57

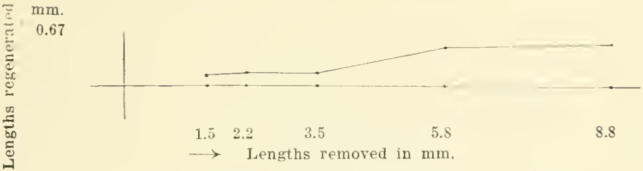

Figure 36 *Amblystoma punctatum* Lengths regenerated Two days

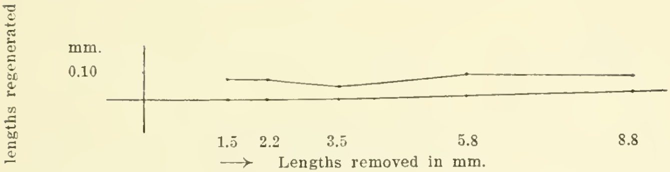

Figure 37 *Amblystoma punctatum* Specific lengths regenerated Two days

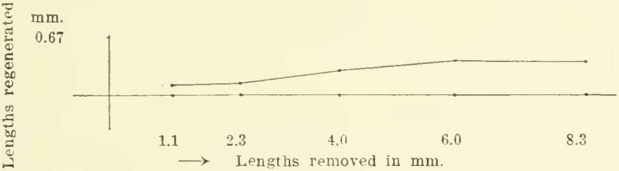

Figure 38 *Amblystoma punctatum* Lengths regenerated Four days

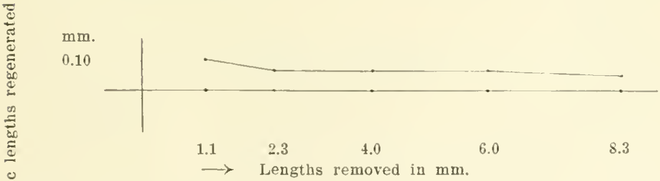

Figure 39 *Amblystoma punctatum* Specific lengths regenerated Four days

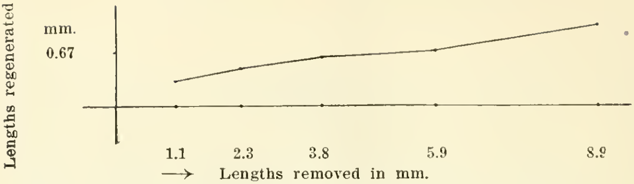

Figure 40 *Amblystoma punctatum* Lengths regenerated Six days

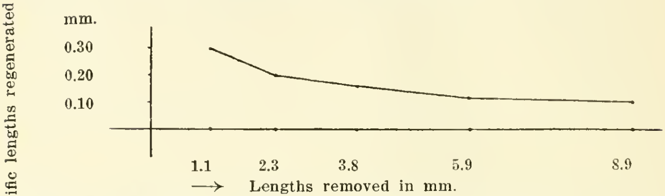

Figure 41 *Amblystoma punctatum* Specific lengths regenerated Six days

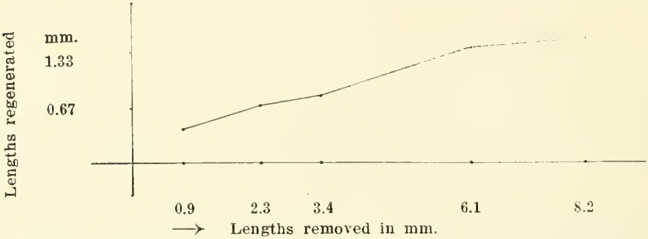

Figure 42 *Amblystoma punctatum* Lengths regenerated Eight to nine days

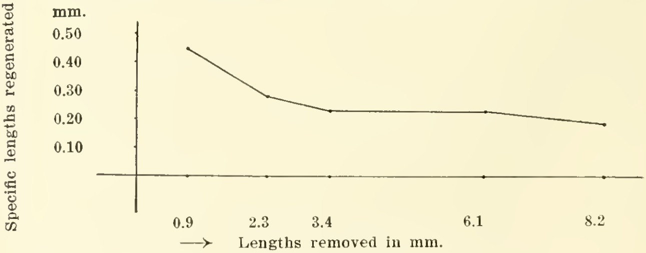

Figure 43 *Amblystoma punctatum* Specific lengths regenerated Eight to nine days

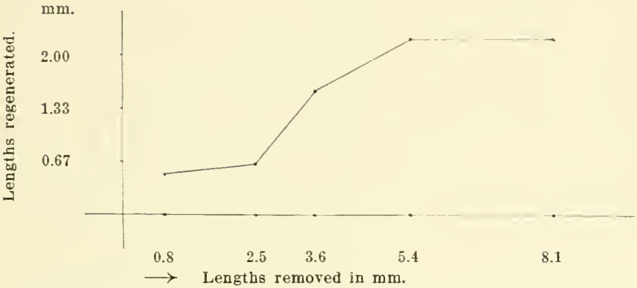

Figure 44 *Amblystoma punctatum* Lengths regenerated Ten to eleven days

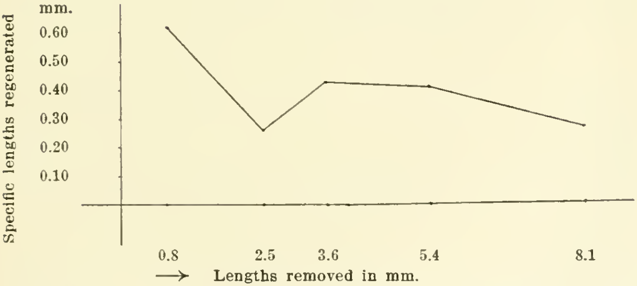

Figure 45 *Amblystoma punctatum* Specific lengths regenerated Ten to eleven days

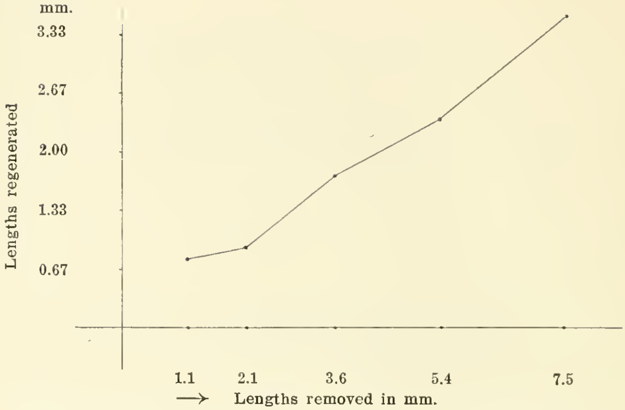

Figure 46 *Amblystoma punctatum* Lengths regenerated Thirteen days

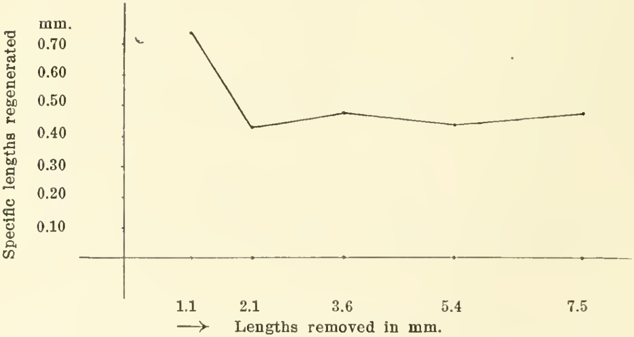

Figure 47 *Amblystoma punctatum* Specific lengths regenerated Thirteen days

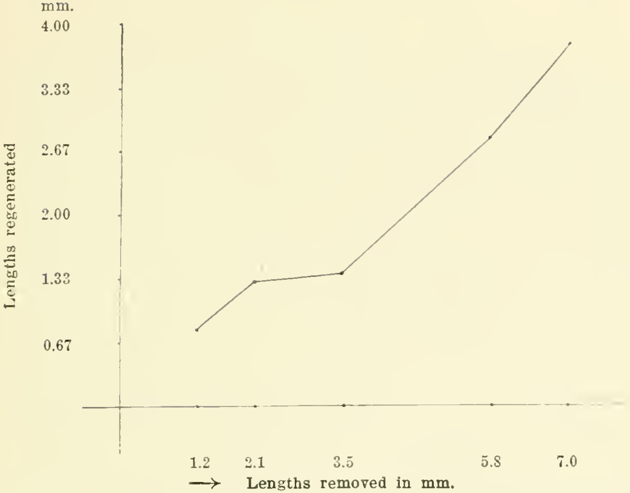

Figure 48 *Amblystoma punctatum* Lengths regenerated Fifteen to sixteen days

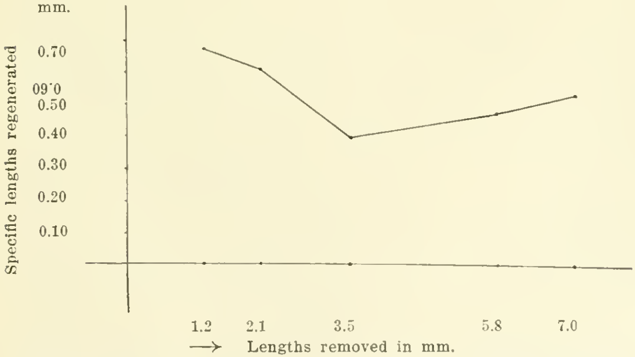

Figure 49 *Amblystoma punctatum* Specific lengths regenerated Fifteen to sixteen days

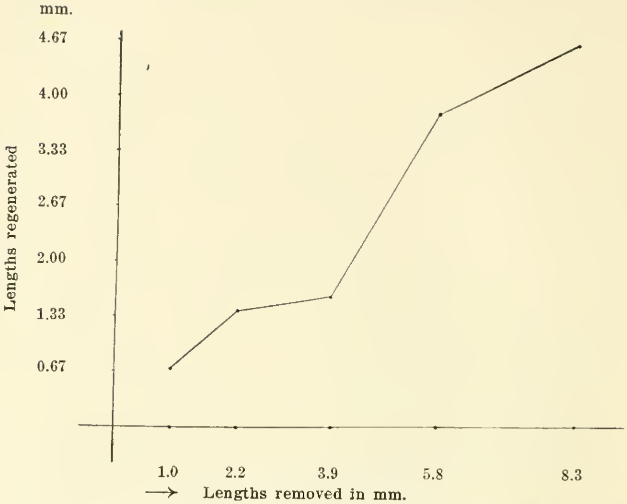

Figure 50 *Amblystoma punctatum* Lengths regenerated Seventeen to eighteen days

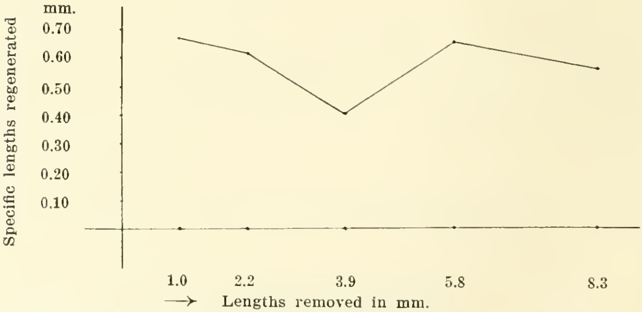

Figure 51 *Amblystoma punctatum* Specific lengths regenerated Seventeen to eighteen days

Discussion

That the level of the cut has an important influence upon the rate of regeneration has been made out by a number of investigators (Spallanzani 1768, King 1898, Morgan 1906, Stockard 1908, Ellis 1909, Morgulis 1909a, b, and others). Their work indicates that regenerations from deeper levels are on the whole more rapid that from more superficial ones. The data obtained from the present experiments confirm this conclusion and make possible a further analysis of the relation. They show that in the regeneration of the tail of amphibian larvae there is a striking relation between the level of the cut and the rate of regeneration. Within wide limits the length regenerated is directly proportional to the distance of the cut surface from the original tip of the tail. Within these limits therefore regeneration at any particular time after the operation has the same degree of completeness from all levels of injury.

An analysis of the progress of the regeneration brings out the fact that two distinct periods are to be recognized in rate of regeneration in its relation to level of the cut. During the first two to four days after the operation regeneration is confined to cell migration from the old tissues without cell division. During this period in the frog tadpoles there is no essential difference in length regenerated at the different levels and the specific rate is therefore much greater after shorter than after longer removals. In the second period with the initiation of rapid cell multiplication the rate of regeneration is greater the deeper the level and furthermore is directly proportional to the length removed. As soon as the bulk of material produced by cell division is considerably greater than that which was produced by cell migration there is an approach to constancy in specific length regenerated. This holds for all except the shortest removals. After the shortest removals the total regeneration is so small in amount that a large part of it is made up of the original migrated material. Therefore from these levels the specific regenerated lengths are greater than from the deeper levels even at a late period of regeneration.

A further complication is introduced by the fact that regeneration is not complete. Only a certain per cent of the removed length is replaced and the end of the process is reached sooner after the shorter than after the longer removals. From the deepest levels regeneration is still proceeding when it has stopped from the medium and shallowest ones. When the process is completed in all cases the specific length is therefore slightly greater after both the longest and the shortest removals than after medium ones.

As to the cause of the difference in rate at the different levels little more can be said than that it does not seem to be due to inherent differences in the cells at the different levels. If differentiation in the tail proceeded from the tip toward the base, the more rapid rate from the more basal levels might be explained by the more embryonic character of the cells at these levels. As the tip is approached the material would become more and more inert. There is however no evidence that differentiation proceeds in this way in this case.

The progressive increase in rate with depth of level of the cut is undoubtedly due to reactions which involve a more central control, a co-ordination of the functional activity as a whole. The period of cell migration probably is only slightly subject to such control. It is a period in which the response is largely local in character and there is correspondingly little if any difference at the different levels. The rate of cell division which is the important factor during the period of rapid increase in length is however undoubtedy under central control.

SUMMARY

1. In frog and salamander larvae with removed tail lengths of one-fifth to two-thirds, the general rule holds that the length regenerated in a given time is proportional to the length removed, or in other words the length regenerated per unit of removed length is a constant.

2. An analysis of the data shows however that this applies only to the material produced by active cell division.

3. During the first four days, in frog tadpoles, when the regenerating part is made up almost entirely of cells that have migrated from the old tissues without division there is no such relation between length removed and length regenerated. The length of new material at this time is not strikingly different for the different levels and the process seems to be a local response of the cells to the injury. The length regenerated per unit of removed length is greater at this time for the shorter than for the longer removals.

4. Since comparatively a large part of the regenerating material after the shorter removals is made up of migrated cells even at the later periods it follows that the specific regenerations from these levels are greater than from the deeper ones.

5. During the later periods the specific regenerated lengths tend to be higher after both the shortest and the longest removals than after medium ones. In the case of the shortest ones this is due to the relatively large part of the whole regenerated tail that is made up of migrated cells. In the case of the longest removals it is due to the fact that regeneration continues for a time after it has stopped in the medium ones.

6. It does not seem probable that the differences in length regenerated at different levels can be due to differences in the original character of the cells involved in the process. Such a well graduated difference in cell capacities is difficult to conceive. The process must be under a more central control, probably connected with general functional activity.

PART IV

THE CHANGE IN RATE OF REGENERATION DURING THE REGENERATIVE PROCESS

The present experiments were undertaken in extension of previous studies on the change in rate throughout the regenerative cycle. This previous work showed that the increase in amount of material during regeneration follows the general rule of increase during an ordinary life cycle. The rate is at first very slow, then increases very rapidly to a maximum, then declines rapidly at first and then more and more slowly as zero is approached.

Frog tadpoles and salamander larvae were used in the present study. Large tadpoles of *Rana clamitans* which remained fairly constant in size during the course of the experiments were found to be the most satisfactory. The results obtained from them were uniform enough for an analysis of the change in rate. The salamander larvae showed a great variation in rate from day to day apparently associated with external factors such as food and temperature. The data obtained from them are however of interest in comparison with the frog tadpole results.

The experiments will be taken up in turn beginning with the series containing the largest number of individuals and giving the most uniform results.

EXPERIMENT I RANA CLAMITANS SECOND REGENERATIONS OF THE TAIL SERIES 3676-3765

The tadpoles were collected on December 9, 1911 and first removals were made on December 22 and second removals on January 8. Measurements were taken 4, 6, 8, 10, 12½ and 56 days after the operation. The operations were made at six different levels, the removals approximating 6, 10, 18, 31, 49 and 67 per cent of the tail length. The first of these removals averaged 1.5 mm. and four individuals with completed measurements are available, the next averaged 2.8 mm. with seven individuals, the third 4.9 mm. with five, the fourth 8.4 mm. with ten, the fifth 13.1 mm. with eight and the sixth 18.1 mm. with ten individuals. The rates per day for each level during each period are given in table 55 and in graphic form in figure 52. The maximum

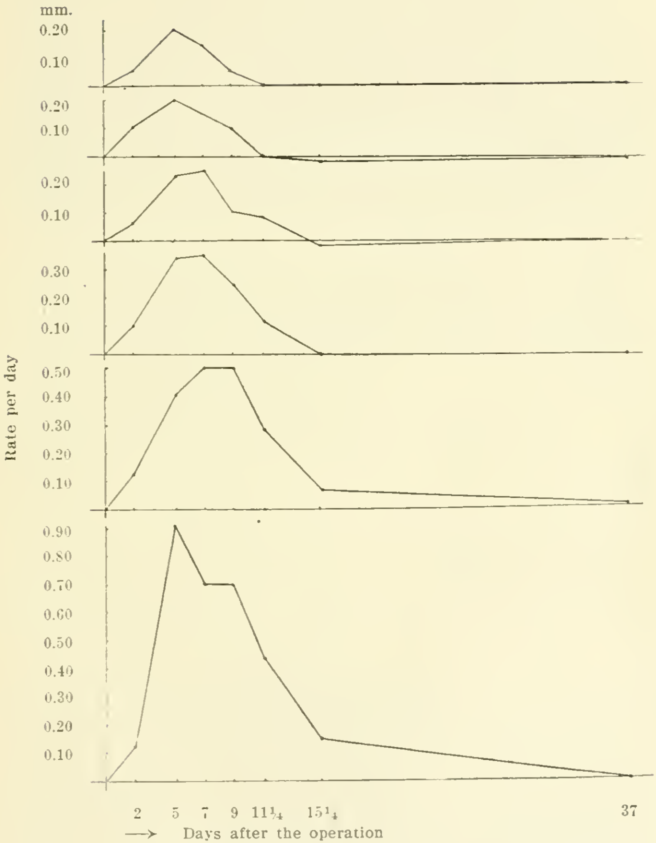

Figure 52 Rates of second regenerations of the tail per day at different times after the operation for six different levels *Rana clamitans* The removed lengths are 1.5, 2.8, 4.9, 8.4, 13.1 and 18.1 mm.

rate is reached during the period between four and six days at three of the levels and between six and eight days at the other three. The rise in rate is very rapid and the decline also rapid.

As discussed in the preceding section on the effect of the level of the cut, the rate of regeneration increases with depth of the level and the increase is such that in general the specific length or length regenerated per unit of removed length is approximately a constant. A reduction of the rates to specific rates therefore gives an opportunity for averaging the different levels together. The resultant average is based upon a sufficiently large number of individuals to give a considerable degree of smoothness in the curve of rate. The data for specific rate are given in Table 56. The average specific rates for all six levels together are 0.019 mm. during the 0 to 4 day period, 0.066 during the 4 to 6 day period, 0.051 for 6 to 8 days, 0.033 for 8 to 10 days, 0.017 for 10 to 12½ days, 0.001 for 12½ to 18 days and —0.001 for 18 to 56 days. This change in rate is represented graphically in the upper part of Figure 53. For the four deepest levels the averages are given in a separate column of Table 56. They exclude the two lowest levels which

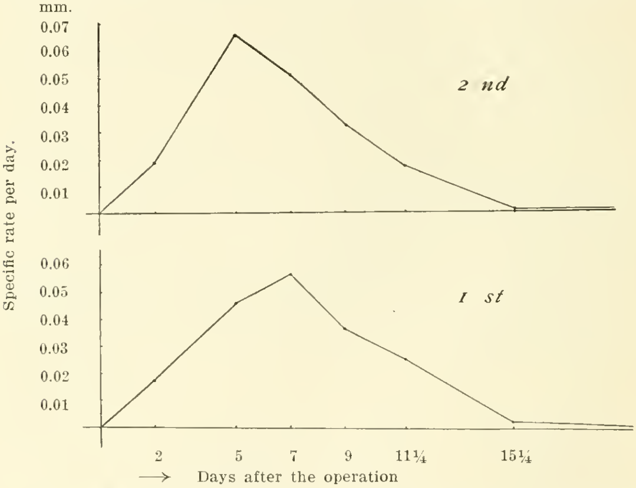

Figure 53. Specific rates of first and second regenerations at different times after the operation *Rana clamitans* Tail regeneration Upper figure, second regenerations; lower, first regenerations.

depart considerably from the others in specific rate. There is however no essential difference in the two sets of values as regards the form of the rate curve.

The change in rate of regeneration or acceleration of rate from any period to the succeeding one is shown in Table 57 in which the period of change is represented by the middle days of the two periods which are being compared. The average of all the levels shows the acceleration to be +0.095 mm. from the 2 to the 5 day period, —0.015 for 5 to 7 days, —0.030 for 7 to 9 days, —0.058 for 9 to 11¼ days, —0.028 for 11¼ to 15¼ days and —0.001 for 15¼ to 37 days. It is only between the first two periods that acceleration of rate is a plus quantity. During all the others it is minus, the most rapid rate of decrease coming between 9 and 11¼ days.

The accelerations of specific rate are more reliable measures for obtaining averages including the different periods. Such values are given in Table 58 and in graphic form in Figure 54. They give a result in the relation of the periods to each other essentially similar to that above. The average accelerations of specific rate are +0.014 for the 2 to 5 day periods, —0.004 for 5 to 7 days, —0.009 for 7 to 9 days, —0.0085 for 9 to 11¼ days, —0.003 for 11¼ to 15¼ days and 0.000 for 15¼ to 37 days. The first period is the only one with a plus acceleration. The greatest minus acceleration comes between the 7 and the 9 day periods instead of 9 to 11¼ days. Averaging only the regenerations for the four deepest levels which show a constant specific rate

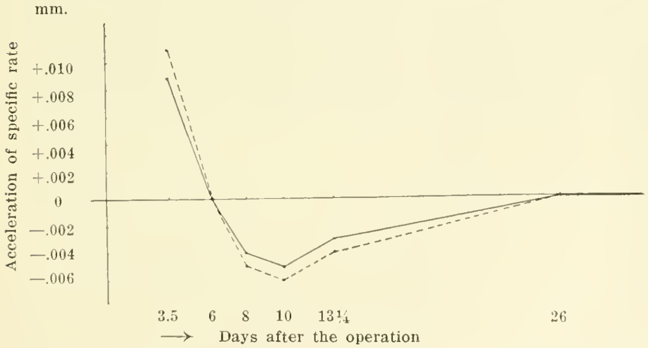

Figure 54. Acceleration of specific rate First and second regenerations of the tail in *Rana clamitans* Unbroken line=First regeneration Broken line=Second regeneration.

the values are respectively +0.011, 0.000, —0.005, —0.006, —0.004 and 0.000, putting the greatest rate of decrease between the 9 and the 11¼ day periods.

An examination of the curves of specific rate and a comparison with the facts of histogenesis shows that acceleration of rate is a plus quantity only during the period before active differentiation of the cells, i. e. until the end of the fifth or seventh day. As soon as tissue differentiation is fairly begun the retarding influence is apparent and by the ninth to eleventh days when muscle fibres and other cells are in full process of differentiation the negative acceleration is at its height.

Following the percentage increment method used by Minot (1908) for ordinary growth and using length instead of weight because the latter could not be determined with sufficient accuracy the results given in Table 59 are obtained. The values for the six periods excluding the first one are 106, 28, 12, 5 and 0. The regenerated material present at the end of four days is made up almost wholly of cells that have migrated from the old tissues and have not as yet undergone division. After the fourth day the additions to regenerated material are almost wholly the result of cell division. From the end of the fourth to the end of the sixth day the material is on the average more than doubled in length each day. After this time the percentage increment decreases rapidly. The change from period to period is represented in graphic form in Figure 55. The curve is a logarithmic one quite similar to that obtained

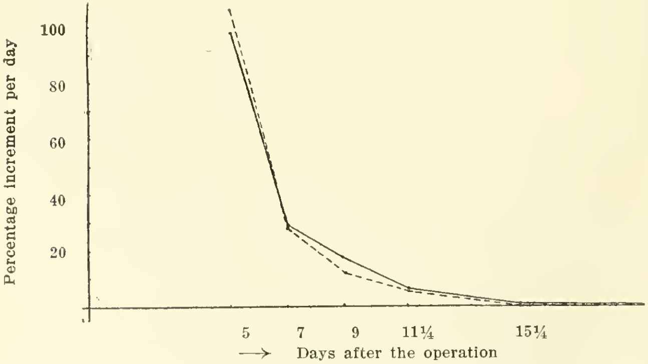

Figure 55 Percentage increment per day at different periods after the operation First and second regenerations of the tail of *Rana clamitans* Unbroken line=first regeneration. Broken line=second regeneration.

by Minot for growth. It should however be pointed out that both regeneration and ordinary growth undoubtedly have a very rapidly ascending branch of the curve if the very beginnings of the processes are included.

TABLE 55

Rana clamitans Series 3676-3765 Second regenerations

Rate of regeneration of tail per day at different times during the regenerative process for six different levels

Percent of tail length removed	6	10	18	31	49	67
Length removed in mm.	1.5	2.8	4.9	8.4	13.1	18.1
No. of individuals	4	7	5	10	8	10
Days 0- 4	0.05	0.10	0.06	0.10	0.12	0.13
4- 6	0.20*	0.20*	0.23	0.34	0.40	0.91*
6- 8	0.14	0.15	0.25*	0.35*	0.50*	0.70
8-10	0.05	0.10	0.10	0.25	0.50*	0.70
10-12½	0.00	0.00	0.08	0.12	0.28	0.44
12½-18	0.00	—0.02	—0.02	0.00	0.07	0.15
18-56	0.00	—0.01	0.00	0.00	0.01	0 00

TABLE 56

Rana clamitans Series 3676-3765 Second regenerations
Specific rates at different levels at different times

Percent of tail length removed	6	10	18	31	49	67	Average of all levels	Average of four longest removals..
Length removed in mm.	1.5	2.8	4.9	8.4	13.1	18.1		
No. of individuals	4	7	5	10	8	10		
Days 0- 4	0.037	0.035	0.012	0.012	0.010	0.007	0.019	0.010
4- 6	0.135*	0.080*	0.045	0.040	0.045*	0.050*	0.066*	0.045*
8-10	0.035	0.035	0.025	0.030	0.035	0.035	0.051	0.042
6- 8	0.090	0.045	0.050*	0.045*	0.040	0.040	0.033	0.032
10-12½	0.000	0.000	0.025	0.015	0.030	0.030	0.017	0.025
12½-18	0.000	—0.005	—0.004	0.000	0.005	0.009	0.001	0.002
18-56	—0.002	—0.004	0.001	0.000	0.001	0.000	—0.001	0.000

TABLE 57

Rana clamitans Series 3676-3765 Second regenerations
Acceleration of rate of regeneration of tail per day at different times during the regenerative process for six different levels

Percent of tail length removed	6	10	18	31	49	67	Average of all levels
Length removed in mm.	1.5	2.8	4.9	8.4	13.1	18.1	
No. of individuals	4	7	5	10	8	10	
Middle of periods Days 2- 5	+0.05*	+0.03*	+0.06*	+0.08*	+0.09*	+0.26*	+0.095*
5- 7	—0.03	—0.02	+0.01	+0.00	+0.05	—0.10	—0.015
7- 9	—0.04*	—0.02	—0.07*	—0.05	0.00	0.00	—0.030
9-11¼	—0.02	—0.04*	—0.01	—0.06*	—0.10*	—0.12*	—0.058*
11¼-15¼	0.00	—0.00	—0.02	—0.03	—0.05	—0.07	—0.028
15¼-37	—0.00	—0.00	+0.00	—0.00	—0.00	—0.01	—0.001

TABLE 58

Rana clamitans Series 3676-3765 First regenerations

Acceleration of specific rate of regeneration of the tail

Percent of tail length removed	6	10	18	31	49	67	Average of all levels	Average of four deepest levels
Length removed in mm.	1.5	2.8	4.9	8.4	13.1	18.1		
No. of individuals	4	7	5	10	8	10		
Days 2- 5	+0.033*	+0.011*	+0.012*	+0.010*	+0.007*	+0.014*	+0.014*	+0.011*
5- 7	—0.020	—0.007	+0.002	0.000	+0.004	—0.006	—0.004	0.000
7- 9	—0.027*	—0.007	—0.014*	—0.006	0.000	0.000	—0.009*	—0.005
9-11¼	—0.013	—0.014*	—0.002	—0.007*	—0.008*	—0.007	—0.008	—0.006*
11¼-15¼	0.000	0.000	—0.004	—0.004	—0.004	—0.004	—0.003	—0.004
15¼-37	0.000	0.000	0.000	0.000	0.000	—0.001	0.000	0.000

TABLE 59

Rana clamitans Series 3676-3765 First regenerations

Percentage increment of regenerating tail per day during each time period for six different levels

Percent of tail length removed	6	10	18	31	49	67	Average of all levels
Length removed in mm.	1.5	2.8	4.9	8.4	13.1	18.1	
No. of individuals	4	7	5	10	8	10	
Days 4- 6	91	53	96	142	80	175	**106**
6- 8	23	19	36	32	29	30	**28**
8-10	5	9	8	14	19	19	**12**
10-12½	0	0	6	5	8	9	**5**
12½-18	0	—2	—1	0	2	2	**0**
18-56	—0	—1	+0	—0	+0	+0	**0**

EXPERIMENT II RANA CLAMITANS FIRST REGENERATIONS OF THE TAIL
SERIES 3676-3765

The tadpoles were collected on December 9, 1911, and the tail removals were made on January 8. Measurements were taken 4, 6, 8, 10, 12½, 18 and 56 days after the operations. The operations were at six levels approximating 6, 10, 17, 30, 48 and 62 per cent of the original tail length. For the first of these levels only two individuals with an average removal of 1.5 mm. are available, for the second five individuals with 2.6 mm., for the third three with 4.6 mm., for the fourth eight with 8.2 mm., for the fifth five with 13.0 mm. and for the sixth five with 16.7 mm. The rates of regeneration per day are given in table 60 and the graphs for the rates in Figure 56.

The specific rates are given in Table 61. Averaging these values so as to include all the different levels for each period the specific rates are 0.018 for 0 to 4 days, 0.046 for 4 to 6 days, 0.057 for 6 to 8 days, 0.037 for 8 to 10 days, 0.026 for 10 to 12½ days, 0.002 for 12½ to 18 days and —0.001 for 18 to 56 days. The graph is shown in the unbroken line in Figure 53. Using only the four deepest levels the average specific rates are respectively 0.013, 0.042, 0.045, 0.036, 0.025, 0.006 and 0.000 giving essentially the same form of curve as for the average of all levels.

The accelerations of rate are shown in Table 62 and the accelerations of specific rate in Table 63 and in the unbroken line of Figure 54. The average accelerations of rate per day are respectively +0.078, 0.000, —0.022, —0.042, —0.025 and 0.000 mm. The average accelerations of specific rate including all levels are respectively +0.011, —0.001, —0.007, —0.0075, —0.003 and 0.000 and including only the four deepest levels, +0.009, 0.000, —0.004, —0.005, —0.003 and 0.000. As for second regenerations the only plus acceleration is between 2 and 5 days and the most rapid decrease takes place between 9 and 11¼ days.

The percentage increments per day are shown in Table 64 and in the unbroken line of Figure 55. The values are respectively 98, 29, 17, 6, 1 and 0 percent per day giving approximately the same form of curve as for second regenerations.

In general the first regenerations agree with the second but on the whole the second regenerations reach their maximum earlier and are more rapid than the first up to the time of maximum rate. The first are more rapid than the second after the maximum.

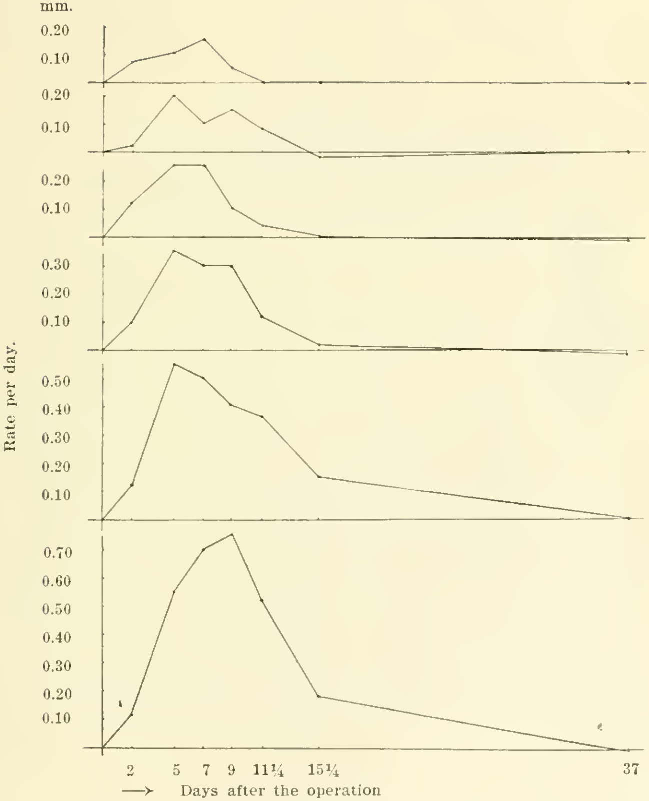

Figure 56 Rates of first regenerations of the tail per day at different times after the operation for six different levels *Rana clamitans* The removed lengths are 1.5, 2.6, 4.6, 8.2, 13.0 and 16.7 mm.

TABLE 60

Rana clamitans Series 3676-3765 First regenerations

Rate of regeneration of tail per day at different times during the regenerative process for six different levels

Percent of tail length removed	6	10	17	30	48	62
Length removed in mm.	1.5	2.6	4.6	8.2	13.0	16.7
No. of individuals	2	5	3	8	5	5
Days 0- 4	0.07	0.02	0.12	0.10	0.12	0.12
4- 6	0.10	0.20*	0.25*	0.35*	0.55*	0.55
6- 8	0.15*	0.10	0.25*	0.30	0.50	0.70
8-10	0.05	0.15	0.10	0.30	0.40	0.75*
10-12½	0.00	0.08	0.04	0.12	0.36	0.52
12½-18	0.00	—0.02	0.00	0.02	0.15	0.18
18-56	—0.01	0.00	—0.01	—0.01	0.00	0.00

TABLE 61.

Rana clamitans Series 3676-3765 Second regenerations
Specific rates at different levels at different times

Percent of tail length removed	6	10	17	30	48	62	Average of all levels	Average of four longest removals
Length removed in mm.	1.5	2.6	4.6	8.2	13.0	16.7		
No. of individuals	2	5	3	8	5	5		
Days 0- 4	0.042	0.015	0.027	0.012	0.007	0.007	**0.018**	**0.013**
4- 6	0.065	0.040	0.055*	0.040*	0.045*	0.030	**0.046**	**0.042**
6- 8	0.115*	0.045	0.055*	0.040*	0.040	0.045*	**0.057***	**0.045***
8-10	0.025	0.055*	0.020	0.035	0.045*	0.045*	**0.037**	**0.036**
10-12½	0.015	0.040	0.010	0.015	0.035	0.040	**0.026**	**0.025**
12½-18	—0.002	—0.007	0.000	0.004	0.011	0.009	**0.002**	**0.006**
18-56	—0.004	—0.001	—0.001	—0.001	0.000	0.000	**—0.001**	**0.000**

TABLE 62

Rana clamitans Series 3676-3765 First regenerations

Acceleration of rate of regeneration of tail per day at different times during the regenerative process for six different levels

Percent of tail length removed	6	10	17	30	48	62	Average of all levels
Length removed in mm.	1.5	2.6	4.6	8.2	13.0	16.7	
No. of individuals	2	5	3	8	5	5	
Middle of periods Days. 2- 5	+0.01	+0.06*	+0.04*	+0.08*	+0.14*	+0.14*	+0.078*
5- 7	+0.02*	—0.05*	0.00	—0.02	—0.02	+0.07	0.000
7- 9	—0.05*	+0.02	—0.07*	0.00	—0.05*	+0.02	—0.022
9-11¼	—0.02	—0.03	—0.02	—0.07*	—0.02	—0.09*	—0.042*
11¼-15¼	0.00	—0.02	—0.01	—0.02	—0.04	—0.06	—0.025
15¼-37	—0.00	0.00	—0.00	—0.00	0.00	+0.00	—0.000

TABLE 63

Rana clamitans Series 3676-3765 First regenerations
Acceleration of specific rate of regeneration of the tail

Percent of tail length removed	6	10	18	31	49	67	Average of all levels	Average of four deepest levels
Length removed in mm.	1.5	2.8	4.9	8.4	13.1	18.1		
No. of individuals	4	7	5	10	8	10		
Days 2- 5	+0.007	+0.023*	+0.009*	+0.010*	+0.011*	+0.008*	+0.011*	+0.009*
5- 7	+0.013*	−0.019*	0.000	−0.002	−0.002	+0.004	−0.001	0.000
7- 9	−0.033*	+0.008	−0.015*	0.000	−0.004*	+0.001	−0.007	−0.004
9-11¼	−0.013	−0.012	−0.004	−0.009*	−0.002	−0.005*	−0.007*	−0.005*
11¼-15¼	0.000	−0.008	−0.002	−0.002	−0.003	−0.004	−0.003	−0.003
15¼-37	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

TABLE 64

Rana clamitans Series 3676-3765 First regenerations

Percentage increment of regenerating tail per day during each time period for six different levels

Percent of tail length removed	6	10	17	30	48	62	Average of all levels
Length removed in mm.	1.5	2.6	4.6	8.2	13.0	16.7	
No. of individuals	2	5	3	8	5	5	
Days 4- 6	33	200	50	87	110	110	98
6- 8	30	20	25	27	31	44	29
8-10	6	21	7	18	23	25	17
10-12½	0	8	2	5	9	12	6
12½-18	0	—2	0	1	3	3	1
18-56	—0	0	—0	—0	0	+0	0

EXPERIMENT III RANA CLAMITANS . FIRST AND SECOND REGENERATIONS OF THE TAIL SERIES 3628-3675

For comparison with the data of experiments I and II it is of interest to note the results obtained from this entirely different series of the same species which was designed primarily for the comparison of first and second regenerations. A full description of the experiment is given in the section on the effect of successive removal upon the rate of regeneration. The data of specific value for present purposes are given in Table 65. Measurements were made only at six and at eight days after the operation. Fifty percent in length of the tail was removed in both first and second regenerations. Twenty- one individuals are available for first and sixteen for second regenerations.

The rates per day are 0.52 mm. for 6 to 8 days for first regenerations as compared with 0.50 for the same period in Experiment II and 0.62 for second regenerations as compared with 0.50 in Experiment I. The specific rate per day for 6 to 8 days for first regenerations is 0.049

and for second regenerations 0.057 as compared with 0.050 for forty eight percent removals in the first regenerations of Experiment II and 0.050 for forty nine percent removals in the second regenerations of Experiment I.

The percentage increments per day are 26 for first regenerations as compared with 29 in Experiment II and 28 for second regenerations as compared with 28 in Experiment I.

The close agreement of these values taken from a comparatively large number of individuals strengthens the conclusion as to the validity of the comparisons at different periods and levels in experiments I and II.

TABLE 65

Rana clamitans Series 3628-3765

First and second regenerations of the tail Six and eight days

	No. of individuals	Total length mm.	Tail length mm.	Percent of length removed	Length removed	Regenerated length Six days	Regenerated length Eight days	Rate per day	Specific rate	Percentage increment per day
First regeneration	21	32.7	21.4	50	10.6	2.01	3.06	0.52	0.049	26
Second regeneration	16	33.4	21.8	50	10.9	2.18	3.42	0.64	0.057	28

Experiment IV Amblystoma punctatum Tail Series 4600-5052

Operations were made at five levels approximating 10, 21, 34, 53 and 74 per cent of the original tail length. The removed lengths average respectively 1.1, 2.2, 3.7, 5.8 and 8.1 mm. Measurements were made 2, 4, 6, 8-9, 10-11, 13, 14-15 and 16-17 days after the operation. The rates per day for each of the levels at each of the different times are given in Table 66.

The specific rates are shown in Table 67. The averages for all the levels at each of the time periods are respectively 0.032 mm. for 0 to 2 days, 0.004 for 2 to 4 days, 0.053 for 4 to 6 days, 0.039 for 6 to 8 days, 0.064 for 8.4 to 10.3 days, 0.043 for 10.3 to 13.0 days, 0.012 for 13.0 to 15.2 days and 0.019 for 15.2 to 17.3 days. As in the case of other salamander experiments the data are more irregular than those for the frog tadpoles because of the susceptibility of the salamander larvae to factors which have not so far been brought under control. The character of the food is probably an important factor. The greatest rate comes between 8.4 and 10.3 days after the operation for three of the five levels and also for the average of all levels. This is later than the maximum for the frog tadpole which comes between four and six days for second regenerations and between six and eight days for first regenerations. The period of decline in rate is also more extended in these salamander larvae than in the frog tadpoles of Experiments I and II.

On account of the irregularity of the data it is not possible to study the acceleration of rate for the present data.

The percentage increments per day are given in Table 68. The values for the seven time periods are respectively 8, 71, 20, 23, 14, 4 and 7. The greatest percentage increment comes between 4 and 6 days as in the case of the frog tadpoles. An earlier period, that between two and four days is represented here. During this period the percentage increment is low. If this value can be accepted the curve here includes the very steep ascending portion discussed above. The irregularities in rate to which the salamander larvae are subject and the fact that the low value during this period does not appear in all the salamander experiments however makes the interpretation doubtful.

TABLE 66

Amblystoma punctatum Series 4600-5052

Rate of regeneration of tail per day at different times during the regenerative process for five different levels

Percent of tail removed	10	21	34	53	74
Length removed. in mm.	1.1	2.2	3.7	5.8	8.1
Days 0-2	0.05	0.07	0.07	0.23	0.26
2-4	0.01	0.00	0.07	—0.03	—0.06
4-6	0.10*	0.16	0.16	0.14	0.27
6-8.4	0.03	0.07	0.07	0.29	0.21
8.4-10.3	0.05	—0.01	0.39*	0.43	0.37
10.3-13.0	0.10*	0.11	0.07	0.07	0.51*
13.0-15.2	0.01	0.17*	—0.17	0.18	0.09
15.2-17.3	—0.05	0.05	0.11	0.48*	0.41

TABLE 67

Amblystoma punctatum Series 4600-5052

Specific rates of regeneration of the tail at different levels at different times after the operation

Percent of tail removed	10	21	34	53	74	**Average of all levels**
Length removed in mm.	1.1	2.2	3.7	5.8	8.1	
Days 0-2	0.035	0.035	0.020	0.040	0.030	**0.032**
2-4	0.020	—0.005	0.015	—0.005	—0.005	**0.004**
4-6	0.095	0.070	0.045	0.025	0.030	**0.053**
6-8.4	0.054	0.033	0.029	0.046	0.033	**0.039**
8.4-10.3	0.100*	—0.011	0.105*	0.095*	0.042	**0.064***
10.3-13.0	0.044	0.063	0.019	0.011	0.078*	**0.043**
13.0-15.2	—0.032	0.081*	—0.036	0.018	0.027	**0.012**
15.2-17.3	0.000	0.005	0 005	0.069	0.014	**0.019**

TABLE 68

Amblystoma punctatum Series 4600-5052

Percentage increment of regenerating tail per day during each time period for five different levels

Percent of tail removed	10	21	34	53	74	Average of all levels
Length removed in mm.	1.1	2.2	3.7	5.8	8.1	
Days 2-4	10	0	50	—6	—12	8
4-6	83*	107*	53*	35	77*	71*
6-8.4	10	16	12	42*	20	20
8.4-10.3	13	—2	49	31	24	23
10.3-13.0	27	17	5	3	23	14
13.0-15.2	1	19	—10	8	3	4
15.2-17.3	—6	4	8	17	11	7

Experiment V Amblystoma punctatum Tail Series 4101-4540

The experiment consists of the regenerations of removed halves of the tail without additional injury in some individuals and with an additional removal of the two forelegs in others. Measurements were made at nine periods, 2, 4, 6, 8, 10, 12, 14, 16 and 19 days after the operation. The rates of regeneration are given in Table 69. The number of individuals for most of the levels is five. The full data are discussed in the section on the effect of degree of injury. The average rate for each of the different times shows that the maximum comes during the eight to ten day period. The high value for the greater degree of injury at 14 to 16 days is due to the death during that period of the two individuals with the lowest values. The result agrees very well with the maximum rate in Experiment IV.

The percentage increments are given in Table 70. The highest value comes during the two to four day period followed by decrease with but little irregularity.

EXPERIMENT VI AMBLYSTOMA PUNCTATUM TAIL SERIES 3962-4004

First, second and third regenerations after removal of approximately one-half of the tail were studied. The complete data are given in the section on the effect of successive removals. Measurements were made at 2, 4, 6, 8, 10 and 14 days. The rates per day are given in Table 71. The maximum rate comes between 8 and 10 days agreeing with the other data for regeneration of the tail in salamander larvae.

The percentage increments are given in Table 72. The highest rate comes at the earliest period, between two and four days, and is followed by a rapid and then a slower decrease.

TABLE 69

Amblystoma punctatum Series 4101-4540

Rate of regeneration per day of tail at different times during the regenerative process for two degrees of injury

Period of regeneration Days	Middle of period Days after operation	Rate of regeneration per day for each period		Average rate
		One-half tail	One-half tail + fore-legs	
0-2	1	0.17	0.13	**0.15**
2-4	3	0.19	0.27	**0.23**
4-6	5	0.29	0.25	**0.27**
6-8	7	0.37	0.47	**0.42**
8-10	9	0.69*	0.50	**0.59***
10-12	11	0.46	0.46	**0.46**
12-14	13	0.23	0.37	**0.30**
14-16	15	0.37	0.53*	**0.45**
16-19	17½	0.16	0.03	**0.09**

TABLE 70

Amblystoma punctatum Series 4101-4540

Percentage increment per day of regenerating tail at different times during the regenerative process for two degrees of injury

Days	Percentage increment per day during each period		Average
	One-half tail	One-half tail+ fore-legs	
2 to 4	54*	100*	77
4 to 6	40	31	35
6 to 8	28	36	32
8 to 10	33	22	27
10 to 12	13	14	13
12 to 14	5	9	7
14 to 16	8	11	9
16 to 19	3	0	1

TABLE 71

Amblystoma punctatum Series 4101-4540

Rate of regeneration per day at different times during the regenerative process

Period of regeneration Days	Middle of period Days after operation	Rate of regeneration per day during each period			Average
		First	Second	Third	
0-2	1	0.11	0.12	0.13	0.12
2-4	3	0.22	0.25	0.37	0.28
4-6	5	0.35	0.32	0.18	0.28
6-8	7	0.41	0.64*	0.66	0.57
8-10	9	0.68*	0.57	0.76*	0.67*
10-14	12	0.45	0.57	0.47	0.50

TABLE 72

Amblystoma punctatum Series 3962-4004

Percentage increment per day at different times during the regenerative process

Days	Percentage increment per day during each period			Average
	First	Second	Third	
2 to 4	100	100	142	114*
4 to 6	53	43	18	38
6 to 8	30	45	48	41
8 to 10	31	21	28	27
10 to 14	12	15	11	13

EXPERIMENT VII AMBLYSTOMA PUNCTATUM FORELEGS
SERIES 4101-4540

The experiment consists of the study of the rate of regeneration of single completely removed fore-legs under three degrees of injury to the individual: without additional injury, with the other fore-leg removed at the same time and with the other fore-leg plus one-half of the tail removed . Measurements were made at 2, 4, 6, 8, 10, 12, 14, 16 and 19 days. The rates of regeneration are given in Table 73. The maximum rate does not come until the 14 to 16 period. The percentage increments are given in Table 74. The highest value comes during the 2 to 4 day period. There is a gradual decrease from this time.

On the whole the data for the leg regeneration show a more extended period than do the tail regenerations.

TABLE 73

Amblystoma punctatum Series 4101-4540

Rate of regeneration per day of fore-leg at different times during the regenerative process for three degrees of injury

Period of regeneration Days	Middle of period Days after operation	Rate of regeneration per day for each period			Average
		One fore-leg	Both fore-legs	Both fore-legs + one-half tail	
0-2	1	0.06	0.08	0.07	0.07
2-4	3	0.04	0.10	0.07	0.07
4-6	5	0.10	0.08	0.13	0.10
6-8	7	0.12	0.15	0.09	0.12
8-10	9	0.12	0.25	0.25	0.21
10-12	11	0.28	0.18	0.18	0.21
12-14	13	0.25	0.29	0.34	0.29
14-16	15	0.52*	0.41*	0.39*	0.44*
16-19	17½	0.27	0.21	0.27	0.25

TABLE 74

Amblystoma punctatum Series 4101-4540

Percentage increment per day of regenerating fore-leg at different periods for three degrees of injury

Days	Percentage increment per day during each period			Average
	One fore-leg	Two fore-legs	Both fore-legs + one-half tail	
2-4	34	62*	46*	47*
4-6	45*	23	45	38
6-8	28	28	16	24
8-10	19	30	35	28
10-12	31	9	15	18
12-14	17	18	21	19
14-16	26	19	17	21
16-19	14	10	13	12

Discussion

The results obtained from the present study show that with certain material it is possible to control disturbing factors so as to get data of a sufficiently uniform nature for an analysis of the change in rate. Such material was found in the tails of the tadpoles of *Rana clamitans*. The analysis has yielded results which should be of value in a determination of the factors involved in the stimulation of growth and more particularly those concerned in slowing it down and finally bringing it to a stop. The characteristics of the change in rate have been studied by means of the curves of rate, of acceleration of rate and of percentage increments. The rate is slow at first, increases rapidly until it is near a maximum at about eight days; then decreases, at first rapidly and then more and more slowly as zero is approached. The acceleration of rate is plus only between the first two periods, i. e., up to the fifth day. After that it is minus, reaching its lowest point at ten days. The percentage increment is very high between the first and second periods but decreases very rapidly at first and then more slowly.

It is evident that there is a close similarity between the change in rate of growth during the regeneration cycle and the change in rate during an ordinary developmental cycle and there is every reason to believe that the factors controlling the one are similar to those controlling the other. The problem of the factors is particularly interesting when it is noted that for widely different levels the rates of regeneration differ in such a way that length regenerated in a given time is proportional to the length removed. The process of regeneration apparently is initiated in a similar manner at each level but is kept under such control that only a certain per cent of the length is regenerated in a given time.

Knowledge of the process is at present insufficient to enable one to discuss with profit the nature of the control of rate of regeneration. All that can be done is to point out the relations of certain phenomena. The initial slow period is coincident with the period of cell migration without cell division, the period of rapidly increasing rate is coincident with the period of rapid cell multiplication without pronounced cell differentiation and the period of rapidly decreasing rate is associated with the appearance of pronounced differentiation in the cells. There is certainly some causal relation between these phenomena.

SUMMARY

1. In second regenerations of the tail in *Rana clamitans* the average specific rates are 0.019 mm. for the 0 to 4 day period, 0.066 for the 4 to 6 day period, 0.051 for 6 to 8 days, 0.033 for 8 to 10 days, 0.017 for 10 to 12½ days, 0.001 for 12½ to 18 days and —0.001 for 18 to 56 days.

2. The average accelerations of rate are +0.095 mm. per day from the first to the second period, —0.015 from the second to the third, —0.030 from the third to the fourth, —0.058 from the fourth to the fifth, —0.028 from the fifth to the sixth and —0.001 from the sixth to the seventh.

3. The average percentage increments between the same periods are respectively 106, 28, 12, 5, 0 and 0.

4. The average accelerations of specific rate for the four deepest levels between the same periods are respectively +0.011 mm., 0.000, —0.005, —0.006, —0.004 and 0.000.

5. In first regenerations of the tail in *Rana clamitans* the average specific rates are 0.018 mm. for 0 to 4 days, 0.046 for 4 to 6 days, 0.057 for 6 to 8 days, 0.037 for 8 to 10 days, 0.026 for 10 to 12½ days, 0.002 for 12½ to 18 days and —0.001 for 18 to 56 days.

6. The average accelerations of rate are +0.078 mm. per day from

the first to the second period, 0.000 from the second to the third, —0.022 from the third to the fourth, —0.042 from the fourth to the fifth, —0.025 from the fifth to the sixth and 0.000 from the sixth to the seventh.

7. The average accelerations of specific rate for the four deepest levels between the same periods are respectively +0.009, 0.000, —0.004, —0.005, —0.003 and 0.000.

8. The average percentage increments between the same periods are respectively 98, 29, 17, 6, 1 and 0.

9. The experiments on salamander larvae show a similar change in rate of regeneration during the process but the number of individuals is too small to allow an analysis of the data.

10. The changes in rate that have been noted bear a definite relation to the histological changes that have been observed during the regeneration of the tail.

PART V

THE EFFECT OF DEGREE OF INJURY UPON THE RATE OF REGENERATION

In a former series of papers the writer gave the results of experiments on the effect of degree of injury upon the rate of regeneration. A number of different species of animals and various combinations of injuries were involved. The results then obtained tend on the whole to show that within certain limits the rate of regeneration from an injured surface is not retarded by simultaneous regeneration in other parts of the body. Where a difference exists between the rates with and without additional injury there is usually an advantage in favor of the part with additional injury. The differences are however often slight and in some of the cases come within the limits of probable error. It is only when the data as a whole are taken that it is possible to judge of the correctness of the general conclusion that within fairly wide limits of additional injury there is certainly no decrease in rate of regeneration but rather a tendency toward an increase.

Some additional data on these points have been obtained in connection with the present study of the factors of regeneration. On the whole they confirm the previous results. The principal experiment (Experiment I) was planned with a view to further analysis of the problem, especially the determination of the effect of additional injury to a like organ as compared with additional injury to an unlike organ.

EXPERIMENT I AMBLYSTOMA PUNCTATUM SERIES 4101-4540

The young were hatched on March 29-April 4, 1913, and the operations were made on May 4 and 5. The measurements of the control individuals at the time of the operations are given in Table 75. The average total length is 31.3 mm., the tail length 14.4 mm., the average length of the fore-legs 3.6 mm. and the average of the hind-legs 1.5 mm.

The measurements of control individuals at the end of the experiment on May 23 are given in Table 76. The total average length is 42.7 mm., the tail length 20.0, the average of the fore-legs 6.2 and the average of the hind-legs 4.5 mm.

The experiment consisted in the determination of the regenerated length of the right fore-leg under three degrees of injury: when the right fore-leg alone is removed, when its mate is also removed and finally when its mate and one-half of the tail are removed. In the last two cases the average of the two fore-legs is taken as the proper value for the regeneration of a fore-leg. A large number of individuals, all hatched from the same lot of eggs, were used and a selection of larvae was made so as to make the experimental animals as nearly alike as possible in this respect. In each of the five sets an individual for each degree of injury was killed at two days after the operation, and also at four, six, eight, ten, twelve, fourteen, sixteen and nineteen days. The data are given in Tables 77 to 88. The three degrees of injury may be represented by (1) R, (2) R+L, (3) R+L+½T, in which R=right fore-leg removed, L=left fore-leg removed and ½T=one-half of the tail removed. The second involves the removal of some additional material of the same kind as that removed in the first. The third as compared with the first involves the removal of some of the same kind of material and some of another kind. In every case it is the regeneration of the fore-leg that is used as the basis of comparison.

The additional simultaneous injury and regeneration does not decrease the regeneration of the individual fore-leg. At two days the average regenerated lengths of a fore-leg are respectively 0.13, 0.16 and 0.15 mm. for the three degrees of additional injury; at four days the corresponding values are 0.22, 0.36 and 0.29; at six days 0.42, 0.53 and 0.55; at eight days 0.66, 0.83 and 0.73; at ten days 0.91, 1.34 and 1.24; at twelve days 1.48, 1.60 and 1.61; at fourteen days 1.98, 2.19 and 2.29; at sixteen days 3.02, 3.01 and 3.08; at nineteen days 3.84, 3.64 and 3.90. At only two of the nine periods is the regeneration of the fore-leg without additional injury as rapid as that of a fore-leg with additional injury and at these two times it is less rapid than one of the two other groups. In seven of the nine cases the regeneration of the fore-leg without additional injury is less than either of the two with such injury.

Among the forty individual comparisons in which all three degrees are present the degree with no additional injury has 6⅚ firsts, the degree with an additional fore-leg 15⅚ firsts and the degree with an additional fore-leg plus one-half of the tail has 17⅓ firsts. Among the nine time groups the degree with no additional injury has 1⅓ firsts and each of the additional injury combinations has 3⅚ firsts.

Taking up the lowest positions in the three degrees in the same way, among the forty individual comparisons the degree with no additional injury gives the lowest regeneration in 21⅓ cases while the additional injury combinations each have only 9⅓ lowest regenerations. Among the nine time groups the degree with no additional injury has the lowest value 6 times, the one with an additional removal of the other fore-leg

2½ times while the one with the highest degree of injury gives the lowest regeneration for the fore-leg only ½ times.

These comparisons show very clearly that the regeneration of a fore-leg is not as rapid when the individual is regenerating no other part at the same time as it is when the other fore-leg is being regenerated at the same time. The additional removal of one-half of the tail does not seem to accelerate the regeneration any further because there is no essential difference between the effect of an additional injury of a fore-leg and an additional injury of a fore-leg plus one-half of the tail. It may be that the effect of additional removal is confined to removal of a similar part, the tail removal in this case involving a different kind of organ. Or it may be that the accelerating effect is found only within certain degrees of injury the limit being exceeding by the highest of the three degrees.

TABLE 75

Amblystoma punctatum Series 4101-4540
Experiment I Controls at beginning of experiment

Date	Catalog number	Total length mm.	Tail length mm.	Fore legs			Hind legs		
				Right	Left	Av'age.	Right	Left	Av'age.
5/4/13	4110	35.0	16.4	4.0	4.0	4.0	3.0	3.1	3.05
5/4/13	4210	31.8	14.8	3.6	3.8	3.7	1.4	1.5	1.45
5/4/13	4310	28.1	11.9	3.3	3.3	3.3	1.0	0.9	0.95
5/4/13	4320	33.8	15.3	3.3	3.1	3.2	1.1	1.0	1.05
5/5/13	4410	30.2	13.8	3.6	3.6	3.6	1.0	1.0	1.0
5/5/13	4510	28.7	14.0	3.9	3.8	3.85	1.4	1.2	1.3
	Average	31.3	14.4			3.6			1.5

TABLE 76
Amblystoma punctatum Series 4101-4540
Experiment I Controls at end of experiment

Date	Catalog number	Total length mm.	Tail length mm.	Fore legs			Hind legs		
				Right	Left	Av'age.	Right	Left	Av'age.
5/23	4120	46.7	24.3	6.1	6.1	6.1	5.0	5.0	5.0
	4130	44.7	21.7	6.5	6.6	6.55	5.2	5.1	5.15
	4140	44.5	20.1	6.5	6.4	6.45	5.2	5.1	5.15
	Average	**45.3**	**22.0**			**6.4**			**5.1**
5/23	4220	43.1	20.1	6.1	6.0	6.05	4.1	4.1	4.1
	4230	45.5	20.6	6.0	6.0	6.0	4.0	5.0	4.5
	4240	43.7	20.4	6.0	5.5	5.75	4.0	4.4	4.2
	Average	**44.1**	**20.4**			**5.9**			**4.3**
5/23	4330	47.2	21.9	7.1	7.2	7.15	5.3	5.2	5.25
	4340	41.5	19.5	6.1	6.2	6.15	4.0	4.1	4.05
	Average	**44.3**	**20.7**			**6.6**			**4.6**
5/23	4420	41.0	18.2	7.0	7.0	7.0	4.9	4.8	4.85
	4430	40.5	19.4	5.6	5.6	5.6	4.0	4.1	4.05
	4440	40.4	18.9	6.0	6.0	6.0	4.1	4.0	4.05
	Average	**40.6**	**18.8**			**6.2**			**4.3**
5/23	4520	36.5	16.0	5.6	5.6	5.6	4.0	4.0	4.0
	4530	40.9	18.5	6.7	6.8	6.75	4.9	4.8	4.85
	4540	40.6	19.1	5.0	5.0	5.0	4.0	4.0	4.0
	Average	**39.3**	**17.9**			**5.8**			**4.3**
Grand	**average**	**42.7**	**20.0**			**6.2**			**4.5**

TABLE 77

Amblystoma punctatum Series 4101-4540

Length of regenerated fore-leg in millimeters for different degrees of injury

Two days

Catalog number	Degree of injury		
	One fore-leg	Both fore-legs	Both fore-legs + one-half tail
4101-11-21	0.10	0.22	0.22
4201-11-21	0.10	0.15*	0.11
4301-11-21	0.10	0.15	0.17*
4401-11-21	0.20	0.17	0.20
4501-11-21	0.15*	0.10	0.07
Average	**0.13**	**0.16***	**0.15**

TABLE 78

Amblystoma punctatum Series 4101-4540

Length of regenerated fore-leg in millimeters for different degrees of injury

Four days

Catalog number	Degree of injury		
	One fore-leg	Both fore-legs	Both fore-legs + one-half tail
4102-12-22	0.25	0.25	0.52
4202-12-22	—	0.52	0.22
4302-12-22	0.15	0.37*	0.22
4402-12-22	0.40*	0.30	0.27
4502-12-22	0.10	—	0.20
Average	**0.22**	**0.36***	**0.29**

TABLE 79

Amblystoma punctatum Series 4101-4540

Length of regenerated fore-leg in millimeters for different degrees of injury

Six days

Catalog number	Degree of injury		
	One fore-leg	Both fore-legs	Both fore-legs + one-half tail
4103-13-23	0.40	0.20	0.92*
4203-13-23	0.50	0.87*	0.52
4303-13-23	0.45	0.65*	0.42
4403-13-23	0.45	0.60*	0.47
4503-13-33	0.30	0.35	0.42*
Average	**0.42**	**0.53**	**0.55***

TABLE 80

Amblystoma punctatum Series 4101-4540

Length of regenerated fore-leg in millimeters for different degrees of injury.

Eight days

Catalog number	Degree of injury		
	One fore-leg	Both fore-legs	Both fore-legs + one-half tail
4104-14-24	0.50	0.75	0.97*
4204-14-24	0.80	0.80	0.80
4304-14-24	0.85	0.87*	0.62
4404-14-24	0.43	0.95*	0.75
4504-14-24	0.70	0.80*	0.52
Average	**0.66**	**0.83***	**0.89***

TABLE 81

Amblystoma punctatum Series 4101-4540

Length of regenerated fore-leg in millimeters for different degrees of injury

Ten days

Catalog number	Degree of injury One fore-leg	 Both fore-legs	 Both fore-legs + one-half tail
4105-15-25	0.25	1.82*	1.60
4205-15-25	0.95	1.10*	1.07
4305-15-25	1.05	1.22	1.32*
4405-15-25	1.20	1.37*	1.07
4505-15-25	1.10	1.20*	1.12
Average	**0.91**	**1.34***	**1.24**

TABLE 82

Amblystoma puuctatum Series 4101-4540

Length of regenerated fore-leg in millimeters for different degrees of injury

Twelve days

Catalog number	Degree of injury One fore-leg	 Both fore-legs	 Both fore-legs + one-half tail
4106-16-26	1.45	1.50	1.77*
4206-16-26	1.35	1.47*	1.44
4306-16-26	1.80*	1.60	1.65
4406-16-26	1.00	1.70*	1.50
4506-16-26	1.80*	1.72	1.67
Average	**1.48**	**1.60**	**1.61***

TABLE 83

Amblystoma punctatum Series 4101-4540

Length of regenerated fore-leg in millimeters for different degrees of injury

Fourteen days

Catalog number	Degree of injury		
	One fore-leg	Both fore-legs	Both fore-legs + one-half tail
4107-17-27	2.60	——	2.25
4207-17-27	1.70	1.97	2.22*
4307-17-27	1.45	1.87	1.95*
4407-17-27	2.25	2.72	2.90*
4507-17-27	1.90	——	2.12
Average	1.98	2.19	2.29*

TABLE 84

Amblystoma punctatum Series 4101-4540

Length of regenerated fore-leg in millimeters for different degrees of injury

Sixteen days

Catalog number	Degree of injury		
	One fore-leg	Both fore-legs	Both fore-legs + one-half tail
4108-18-28	2.60	2.60	2.70*
4208-18-28	2.40	2.62*	2.22
4308-18-28	2.80	2.67	2.85*
4408-18-28	3.60	3.57	3.65*
4508-18-28	3.70	3.57	3.97*
Average	3.02	3.01	3.08*

TABLE 85

Amblystoma punctatum Series 4101-4540

Length of regenerated fore-leg in millimeters for different degrees of injury

Nineteen days

Catalog number	Degree of injury One fore-leg	Both fore-legs	Both fore-legs + one-half tail
4109-19-29	4.00*	3.72	3.95
4209-19-29	3.65	4.05	4.25*
4309-19-29	3.60	2.85	3.60
4409-19-29	4.10*	3.95	3.80
Average	**3.84**	**3.64**	**3.90***

TABLE 86

Amblystoma punctatum Series 4101-4540

Length of regenerated fore-leg in millimeters for different degrees of injury

Summary Two to nineteen days

Days	Degree of injury One fore-leg	Both fore-legs	Both fore-legs + one-half tail
2	0.13	0.16*	0.15
4	0.22	0.36*	0.29
6	0.42	0.53	0.55*
8	0.66	0.83*	0.73
10	0.91	1.34*	1.24
12	1.48	1.60	1.61*
14	1.98	2.19	2.29*
16	3.02	3.01	3.08*
19	3.84	3.64	3.90*
Groups first	0	4	5
Groups last	7	2	0

TABLE 87

Amblystoma punctatum Series 4101-4540

Length of regenerated fore-leg for different degrees of injury

Tabulation of firsts for individual comparisons

Days	Injury		
	One fore-leg	Both fore-legs	Both fore-legs + one-half tail
2	1½	1½	2*
4	1	1	1
6	0	3*	2
8	⅓	3⅓*	1⅓
10	0	4*	1
12	2	2	1
14	0	0	3*
16	0	1	4*
19	2	0	2
Total firsts	6⅚	15⅚	17⅓
Groups first	1⅓	3⅚	3⅚

TABLE 88

Amblystoma punctatum Series 4101-4540

Length of regenerated fore-leg for different degrees of injury

Tabulation of lowest values for individual comparisons

Days	Injury		
	One fore-leg	Both fore-legs	Both fore-legs + one-half tail
2	3	1	1
4	1½	1½	1
6	3	1	1
8	2⅓	⅓	2⅓
10	4	0	1
12	3	1	1
14	3	0	0
16	½	3½	1
19	1	2	1
Total lasts	21⅓	9⅓	9⅓
Groups last	6	2½	½

EXPERIMENT II AMBLYSTOMA PUNCTATUM SERIES 4101-4540

This experiment deals with the same series of individuals as Experiment I. The comparison in this case however is one between the regeneration of the removed half of the tail when it alone is removed and its regeneration when there is an additional removal of the two fore-legs. The data are given in Tables 89 to 99. At two days the regeneration of the tail without an additional injury is 0.35 mm. and with an additional injury 0.27. The corresponding values at 4 days are 0.73 and 0.81, at 6 days 1.32 and 1.31, at 8 days 2.06 and 2.26, at ten days 3.44 and 3.27, at twelve days 4.36 and 4.20, at fourteen days 4.82 and 4.94, at sixteen days 5.57 and 6.00 and at nineteen days 5.90 and 6.06. The regenerating tail with no additional injury is ahead at four times and the one with additional injury is ahead five times. In thirty three individual comparisons the group with no additional injury is ahead seventeen times and the additional injury group sixteen times. Taking the individual cases by time groups the individuals with no additional injury are ahead 5½ times and those with an additional injury 3½ times.

These comparisons show no advantage of one combination over the other. The additional removal of the fore-legs does not retard nor does it accelerate the regeneration of the tail. This result strengthens the view that the acceleration in Experiment I is probably due to the additional removal of material similar to that whose rate is being studied.

TABLE 89

Amblystoma punctatum Series 4101-4540

Length of regenerated tail in millimeters for different degrees of injury

Two days

Catalog number	Degree of injury: One-half tail	Degree of injury: One-half tail + fore-legs
4131-21	0.55*	0.15
4231-21	—	0.35
4331-21	0.35*	0.25
4431-21	0.30	0.30
4531-21	0.20	0.30*
Average	**0.35***	**0.27**

TABLE 90

Amblystoma punctatum Series 4101-4540

Length of regenerated tail in millimeters for different degrees of injury

Four days

Catalog number	Degree of injury: One-half tail	Degree of injury: One-half tail + fore-legs
4132-22	0.45	1.00*
4232-22	0.90	0.90
4332-22	0.50	0.60*
4432-22	1.10*	0.95
4532-22	0.70*	0.60
Average	**0.73**	**0.81***

TABLE 91

Amblystoma punctatum Series 4101-4540

Length of regenerated tail in millimeters for different degrees of injury

Six days

Catalog number	Degree of injury	
	One-half tail	One-half tail + fore-legs
4133-23	1.60	——
4233-23	0.90	1.00*
4333-23	1.70*	1.65
4433-23	1.10	1.50*
4533-23	——	1.10
Average	1.32*	1.31

TABLE 92

Amblystoma punctatum Series 4101-4540

Length of regenerated tail in millimeters for different degrees of injury

Eight days

Catalog number	Degree of injury	
	One-half tail	One-half tail + fore-legs
4134-24	2.40	2.60*
4234-24	1.80	1.90*
4334-24	1.80	2.26*
4434-24	2.70*	2.30
4534-24	1.60	——
Average	2.06	2.26*

TABLE 93

Amblystoma punctatum Series 4101-4540

Length of regenerated tail in millimeters for different degrees of injury

Ten days

Catalog number	Degree of injury One-half tail	 One-half tail + fore-legs
4135-25	3.65*	3.20
4235-25	——	2.55
4335-25	3.20	1.46
4435-25	3.65*	3.20
4535-25	3.25	4.15*
Average	**3.44***	**3.27**

TABLE 94

Amblystoma punctatum Series 4101-4540

Length of regenerated tail in millimeters for different degrees of injury

Twelve days

Catalog number	Degree of injury One-half tail	 One-half tail + fore-legs
4136-26	4.10	4.20*
4236-26	4.70*	3.55
4336-26	4.20*	3.50
4436-26	4.60*	4.50
4536-26	4.20	5.25*
Average	**4.36***	**4.20**

TABLE 95

Amblystoma punctatum Series 4101-4540

Length of regenerated tail in millimeters for different degrees of injury

Fourteen days

Catalog number	Degree of injury One-half tail	 One-half tail + fore-legs
4137-27	4.80	6.00*
4237-27	4.90*	4.70
4337-27	5.00*	4.95
4437-27	4.90*	4.00
4537-27	4.50	5.05*
Average	4.82	4.94*

TABLE 96

Amblystoma punctatum Series 4101-4540

Length of regenerated tail in millimeters for different degrees of injury

Sixteen days

Catalog number	Degree of injury One-half tail	 One-half tail + fore-legs
4138-28	6.50*	5.50
4238-28	5.80	——
4338-28	5.00	6.40*
4438-28	5.00	——
4538-28	8.00	6.10
Average	5.57	6.00*

TABLE 97

Amblystoma punctatum Series 4101-4540

Length of regenerated tail in millimeters for different degrees of injury

Nineteen days

Catalog number	Degree of injury	
	One-half tail	One-half tail
4139-29	6.90*	5.90
4239-29	3.20	6.20
4339-29	——	5.55
4439-29	4.90	6.60*
Average	**5.90**	**6.06***

TABLE 98

Amblystoma punctatum Series 4101-4540

Length of regenerated tail in millimeters for different degrees of injury

Summary Two to nineteen days

Days	Degree of injury	
	One-half tail	One-half tail + fore-legs
2	0.35*	0.27
4	0.73	0.81*
6	1.32*	1.31
8	2.06	2.26*
10	3.44*	3.27
12	4.36*	4.20
14	4.82	4.94*
16	5.57	6.00*
19	5.90	6.06*
Groups first	4	5

TABLE 99

Amblystoma punctatum Series 4101-4540
Length of regenerated tail for different degrees of injury
Tabulation of firsts for individual comparisons

Days	Injury	
	One-half tail	One-half tail + fore-legs
2	2½*	1½
4	2½	2½
6	1	2*
8	1	3*
10	2*	1
12	3*	2
14	3*	2
16	1	1
19	1	1
Total firsts	17	16
Groups first	5½	3½

EXPERIMENT III AMBLYSTOMA PUNCTATUM SERIES 4005-4008

Experiments III, IV, V and VI comprise merely a few individual comparisons obtained from experiments devised principally for the study of other factors. They are included here under the rule that no valid data on the matter at hand are to be excluded.

In Experiment III the regeneration of the hind-leg is compared under the four conditions of (1) no additional injury, (2) removal of the other hind-leg, (3) removal of the other hind-leg and one fore-leg and (4) removal of the other hind-leg and both fore-legs. The data are given in Table 100.

Three sets of comparisons were made at twelve days after the operations, each with a single individual for each degree of injury. The regenerating hind-leg with no additional injury is distinctly behind the cases with additional injury. The greatest regenerated length comes in one case with an additional injury of one hind-leg plus one fore-leg and in two cases with one hind-leg plus two fore-legs. The averages beginning with the lowest degree of injury are respectively 1.50, 1.73, 1.86 and 1.88 mm.

The additional removals are in every case removals of leg material and the result agrees with that of experiment I in giving an increased rate of regeneration of a part when similar organs are removed at the same time.

TABLE 100

Amblystoma punctatum Series 4005-4008

Length of regenerated hind leg in millimeters for different degrees of injury

Twelve days

Catalog number	Degree of injury			
	One hind-leg	Both hind-legs	Both hind-legs+one fore-leg	Both hind-legs+both fore-legs
4005	1.35	1.90	1.95*	1.75
4006	1.65	1.80	1.82	1.92*
4008	1.50	1.50	1.80	1.85*
Average	1.50	1.73	1.86*	1.84

TABLE 101

Amblystoma punctatum Series 4005-4008

Length of regenerated fore-leg in millimeters for different degrees of injury

Twelve days

Catalog number	Degree of injury	
	One fore-leg + both hind-legs	Both fore-legs + both hind-legs
4005	3.0*	2.8
4006	3.1*	3.0
4008	3.0	3.15*
Average	3.07*	2.98

EXPERIMENT IV AMBLYSTOMA PUNCTATUM SERIES 4005-4008

In this experiment the regeneration of the right fore-leg is compared under conditions of differing degrees of additional injury. In one combination there is an additional removal of the two hind legs and in the other of both hind-legs plus the remaining fore-leg. The data are given in Table 101. In two of the three cases the smaller additional degree of injury shows the greater regeneration of the fore-leg. The average is 3.07 mm. for the lesser degree and 2.98 for the greater degree, an advantage in favor of the lesser degree.

It should be noted that this is not strictly comparable with the main issue of Experiments I, II and III. Aside from the small number of cases it is a comparison between two degrees of injury each of which is of considerable extent. It may be that the removal of three of the four legs is near the degree of injury yielding the maximnm rate for each removed leg.

Experiment V Amblystoma punctatum Series 4010-4025

A comparison is made between the regeneration of a half of the tail when it alone is removed and when both fore-legs are removed at the same time. Four individual comparisons are made at fourteen days. The data are given in Table 102. The regenerated lengths and specific lengths regenerated are ahead in two of the four cases for each of the degrees of injury. The average regenerated length with no additional injury is 5.1 mm. and with additional injury 5.0 mm. The specific regenerated length is 0.65 with no additional injury and 0.68 with addi-

TABLE 102
Amblystoma punctatum Series 4010-4025
Regeneration of tail for different degrees of injury
Fourteen days

	Degree of injury					
	One-half tail			One-half tail + both fore-legs		
Catalog number	Length removed	Length regenerated	Specific amt. regenerated	Length removed	Length regenerated	Specific amt. regenerated
4014-13	7.7	4.9	0.64	7.0	5.2*	0.74*
4018-17	8.8	5.2*	0.59*	8.0	4.3	0.54
4022-21	8.0	5.3*	0.66*	8.0	5.1	0.64
4025-24	7.0	4.9	0.70	6.6	5.3*	0.80*
Average		5.1	0.65		5.0	0.68

tional injury. The data show essential equality between the rates of regeneration under the two conditions of the experiment. This agrees with the data in Experiments I and II which show no increase or decrease in rate of regeneration when unlike material is removed simultaneously with the removal of the organ whose rate is being studied.

EXPERIMENT VI AMBLYSTOMA PUNCTATUM SERIES 4010-4025

Three individual comparisons were made at fourteen days of the right fore-leg, when it alone is removed, when the other fore-leg is also removed and when the other fore-leg plus one half of the tail is removed. The data are given in Table 103. In two of the three cases the individuals with no additional regeneration are ahead of the others. The greater injury gives the greater rate in one of the three. The average regenerated lengths beginning with the lowest degree of injury are respectively 1.99, 1.73 and 1.92 mm. The few cases may be a sufficient explanation of the lack of agreement with the more extended series of Experiment I.

TABLE 103

Amblystoma punctatum Series 4010-4025

Length of regenerated fore-leg in millimeters for different degrees of injury

Fourteen days

Catalog number	Degree of injury		
	One fore-leg	Both fore-legs	Both fore-legs + one-half tail
4011, 12, 13	2.00*	1.77	1.65
4015, 16, 17	2.00*	1.60	1.80
4019, 20, 21	1.95	1.82	2.22*
4023, —, 24	2.00	——	2.00
Average	1.99*	1.73	1.92

DISCUSSION

The experiments as a whole show that a part regenerates slightly more rapidly when additional material of the same kind is removed than when the part alone is removed. Simultaneous removal of tail material does not accelerate the regeneration of a leg nor does simultaneous removal of a leg accelerate the regeneration of the tail. The rate in these cases however is not decreased by the additional injury. The statement may therefore be made that within limits the regeneration of a part is not retarded by simultaneous removal and regeneration of material in other parts of the body. When this additional material is of the same kind as that whose rate is being studied there may even be an acceleration of regeneration.

In comparison with such a factor as level of the cut this difference in rate is slight and no such quantitative relation as in that case can be made out. It must however be considered that the principal object of the original experiments was to show that additional injury within the given limits tends to *increase rather than decrease* the rate of regeneration. This has been proved for these experiments. The evidence in favor of a definite increase in rate with any certain increase in degree of injury is not so conclusive. It is obvious that in many series of experiments factors whose influence is greater than that of the factor under discussion may obscure the result.

Emphasis should again be placed on the fact that all data obtained by the writer are included. That some of the series, especially those with a few individuals, diverge from the general result is to be expected by anyone in similar work who has attempted to eliminate entirely all of the factors except the one under observation at a particular time.

SUMMARY

1. A comparison was made of the rate of regeneration of a leg or of the tail of an Amblystoma larva when the part alone is removed with its rate when similar or dissimilar parts of the individual are removed at the same time. The data are derived from two principal Experiments, I and II, and from a few scattered observations listed as Experiments III to VI.

2. In Experiment I a comparison was made of the rate of regeneration of the right fore-leg when it alone is removed with its rate when the other fore-leg is removed at the same time and when the other fore-leg and one half of the tail are removed. The result obtained from forty individual comparisons made at different times shows that the rate of regeneration of the right fore-leg in each of the series with additional injury is greater than in the series without additional injury.

3. The rate of regeneration of a right fore-leg when its mate plus one-half of the tail is removed is not essentially different from the rate when its mate alone is removed. The addition of the injury to a dissimilar organ, the tail, does not alter the rate of regeneration of the fore-legs.

4. In Experiment II it is shown that there is no significant difference between the rate of regeneration of a tail one-half of which has been

removed without additional injury to the individual and the rate after the same injury plus a removal of both fore-legs.

5. The data of Experiments III to VI show some departures from the general rule probably because they deal with few individuals. On the whole however they bear out the results obtained from the principal experiments.

PART VI

THE COMPLETENESS OF REGENERATION

One of the striking facts in connection with amphibian regeneration as made out in the present studies is the lack of completeness of the process. When a part of the tail is removed the lost part is never completely restored. Data on this problem are to be found in a number of sets of experiments one of which (Experiment V) was devised especially for the present purpose.

Experiment I Rana clamitans Series 3557-3624

One-half of the tail was removed in the individuals of three groups, A, B and C. After 35 to 39 days, which was sufficiently long so that regeneration had stopped, another removal was made and so on until each individual had undergone five regenerations. The data are given in Table 104. The average removed length as estimated from the measurement of a few individuals was 17.0 mm. The average length of the completed first regeneration is 8.6 mm. or 51 per cent of the removed length, of the second regeneration 8.0 mm. or 53 per cent, of the third 7.5 mm. or 51 per cent, of the fourth 5.5 mm. or 42 per cent and of the fifth 6.4 mm. of 45 per cent. On the average about one-half of the removed length is replaced when one-half of the tail length is removed.

Experiment II Rana clamitans Series 3628-3675

One-half of the tail length was removed in the individuals of this experiment and regeneration was allowed to proceed for twenty days, a sufficient time for bringing it to a stop. The data are given in Table 105. The average original tail .length was 21.8 mm., of the removed length 10.6 mm. and of the regenerated length 5.4 mm. The completed regenerated length is thus 51 per cent of the removed length.

Experiment III Rana clamitans First regenerations
Series 3676-3765

The data are given in Table 106. The tails were removed at different levels approximating 6, 10, 17, 30, 48 and 62 per cent of the tail lengths. Regeneration was completed at these levels at 12½, 12½, 12½, 18, 18 and 56 days respectively. The regenerated lengths at these times of completion are respectively 61, 46, 39, 33, 42 and 41 per cent of the removed lengths. It will be noted that the two shortest removals give the highest per cents and the two medium ones the lowest per cents. This difference is discussed in Part III on the effect of level of the cut.

EXPERIMENT IV RANA CLAMITANS SECOND REGENERATIONS

SERIES 3676-3765

The data are given in Table 107. The tail was removed at different levels approximating 6, 10, 18, 31, 49 and 67 per cent of the removed lengths. Regeneration was completed for these levels at 10, 10, 12½,

TABLE 104

Rana clamitans Series 3557-3624 Completeness of regeneration Successive regenerations in single individuals One-half of tail removed = 17 mm. on the average First operation Oct. 23, 1911 Second operation Groups A and B Nov. 18 Group C Nov. 28

	Catalog number	First regeneration	Second regeneration	Third regeneration	Fourth regeneration	Fifth regeneration
		Nov. 28	Jan. 3	Feb. 9	Mar. 16	April 24
Group A	3564		9.5	8.5	—	—
	3565		9.8	11.4	7.3	8.2
	3566		10.0	9.3	8.1	6.3
	3567		11.9	9.5	8.0	11.9
	3568		8.4	9.9	11.0	8.5
	3569		10.0	8.7	8.0	8.1
	3570		8.7	8.1	—	—
	Average		9.8	9.3	8.5	8.6
Group B	3578		8.3	9.0	5.8	8.2
	3579		8.2	8.1	11.3	7.0
	3580		11.9	7.3	6.9	8.1
	3581		9.7	8.0	7.6	11.6
	3582		8.3	12.8	7.4	5.4
	3583		8.8	7.4	5.0	6.8
	3584		8.8	9.5	6.4	—
	Average		9.1	8.9	7.2	7.8

TABLE 104 (Continued)

	Catalog number	First regeneration	Second regeneration	Third regeneration	Fourth regeneration	Fifth regeneration
		Nov. 28	Jan. 3	Feb. 9	Mar. 16	April 24
Group C	3586	8.1	—	—	—	—
	3588	6.1	7.5	7.3	5.7	7.2
	3590	8.5	6.6	7.5	5.1	6.5
	3592	7.1	8.0	5.7	4.9	6.5
	3594	8.6	7.8	2.0	5.0	6.1
	3596	9.0	8.6	9.4	6.7	6.8
	3598	10.7	9.7	9.3	6.1	6.2
	3600	8.2	8.0	6.9	5.8	5.9
	3602	9.9	7.7	6.8	4.4	4.7
	3604	9.6	7.6	6.6	4.9	5.7
	3606	7.4	7.8	8.0	5.0	5.9
	3608	9.0	8.0	9.0	5.5	6.9
	3610	8.5	8.9	8.3	5.4	7.1
	3612	7.4	7.0	7.1	4.8	5.5
	3614	8.3	6.6	6.2	4.5	5.2
	3616	8.0	8.3	7.9	6.1	7.9
	3618	9.7	9.5	9.7	7.3	8.0
	3619	—	8.0	7.5	6.6	6.1
	3622	10.2	8.5	—	—	—
	3624	9.3	7.5	—	—	—
	Average	8.6	8.0	7.5	5.5	6.4
Percent of removed length regen. Av.		51	53	51	42	45

12½, 56 and 56 days respectively. The regenerated lengths at these times of completion are respectively 67, 46, 33, 31, 40 and 39 per cent of the removed lengths. As in the case of the first regenerations the two shortest removals give the highest per cent of regeneration and the two medium removals the lowest per cent.

EXPERIMENT V AMBLYSTOMA PUNCTATUM SERIES 6212-6281

The experiments on tadpoles of *Rana clamitans* having shown that only a half or less of the removed length on the average is completed during regeneration it became a matter of interest to see if this might not have been due to the age of the tadpoles, which were obtained in the fall. Accordingly a series of Amblystoma larvae was operated upon within a few days after they had left the egg envelopes and was kept until the salamanders were well advanced in their metamorphosis. Since in young salamander larvae the border line between old and regenerated tissue is soon obliterated it became necessary to devise another method of testing completeness of regeneration than the direct measurement of the regen-

TABLE 105

Rana clamitans Series 3628-3675

Tail length	Removed length	Regenerated length Twenty days
24.1	13.1	5.9
24.6	13.2	5.2
22.1	11.0	4.9
23.2	11.1	5.5
23.1	11.7	5.9
25.0	12.5	5.8
20.4	9.9	5.6
20.8	10.0	5.2
29.2	15.5	5.9
23.8	10.5	5.6
23.3	10.9	5.6
25.6	10.9	5.9
20.8	10.1	4.7
19.2	9.8	4.6
21.1	11.5	5.5
22.0	11.8	6.1
17.0	8.2	5.6
19.0	9.7	5.5
22.4	9.8	4.3
19.8	10.1	5.2
20.8	8.4	5.1
21.8	9.1	5.0
15.4	7.3	6.0
18.1	9.0	6.0
21.8	10.6	5.4
Percent removed	49	
Percent of removed part regenerated		51

TABLE 106

Rana clamitans Series 3676-3765 First regenerations

Number of cases	Percent of tail length removed Average	Tail length removed in mm. Average	Average maximum regeneration in percent of removed length	Average maximum regeneration in mm.	Days after operation when maximum is reached Average
2	6	1.5	61	0.9	12½
5	10	2.6	46	1.2	12½
3	17	4.6	39	1.8	12½
8	30	8.2	33	2.7	18
5	48	13.0	42	5.5	18
5	62	16.7	41	6.9	56

TABLE 107

Rana clamitans Series 3676-3765 Second regenerations

Number of cases	Percent of tail length removed Average	Tail length removed in mm. Average	Average maximum regeneration in percent of removed length	Average maximum regeneration in mm.	Days after operation when maximum is reached Average
4	6	1.5	67	1.0	10
7	10	2.8	46	1.3	10
5	18	4.9	33	1.6	12½
10	31	8.4	31	2.6	12½
8	49	13.1	40	5.2	56
10	67	18.1	39	7.1	56

erated material. This consisted in a comparison of the ratio between tail length and body length in the operated individuals with that in control unoperated individuals. This was done after regeneration had been going on during the whole larval period. If the $\frac{\text{tail}}{\text{body}}$ period is the same in operated as in unoperated individuals it is proper to suppose that regeneration has been complete. If however the ratio is lower the conclusion that regeneration is incomplete is very probably correct though absolute certainty can not be assumed because of the possibility of the changed ratio being due to regulatory changes in other parts of the individual.

The experiment consists of a comparison of the relative degree of completeness of regeneration of the tail in four groups, (1) with no operation, (2) with one-fourth of the tail removed, (3) with one-half of the tail removed and (4) with three-fourths removed. The operations were made as soon as possible after the animals left the egg envelopes and the experiment proceeded until all four legs were well developed and absorption of the gills had begun. This allowed practically the entire larval period for regeneration. There were seventy individuals at the start but a high mortality reduced the number very considerably. Limnodrilus was used as food.

The data are given in Tables 108 to 112. The average ratio between tail and body length in control individuals at the end of the experiment is 1.09, in individuals with one-fourth of the tail removed it is 1.01, in those with one-half removed 0.93 and with three-fourths removed 0.86. This progressive relative decrease in the tail length as compared with the body length is very probably due to lack of completeness of regeneration even though the whole larval period has been allowed for such completion.

Discussion

Apart from the starting stimulus in regeneration the most interesting problem is undoubtedly that of the stopping stimulus. With the growth once started what are the factors involved in checking it? In general it has been assumed that regeneration goes on until the removed organ is entirely replaced and that over- and under-regeneration occur but rarely. The present data make it probable that incompleteness is more general than has been supposed. The factors at work in bringing regeneration to a close tend to overdo rather than underdo their function.

A further investigation of the problem of completeness of regeneration would be of interest.

TABLE 108

Amblystoma punctatum Series 6212-6281 Controls

Catalog number	Living lengths Beginning of experiment April 19 1915				Killed lengths End of experiment June 19 1915			
	Total length	Tail length	Body length	Ratio, $\frac{\text{Tail}}{\text{Body}}$	Total length	Tail length	Body length	Ratio, $\frac{\text{Tail}}{\text{Body}}$
6218	14.1	6.3	7.8	0.81	27.8	14.5	13.3	1.09
6222	13.7	6.0	7.7	0.78	27.2	14.4	12.8	1.12
6223	13.7	6.0	7.7	0.78	32.4	16.9	15.5	1.09
6233	15.0	6.7	8.3	0.81	33.2	17.4	15.8	1.10
6237	14.3	6.0	8.3	0.72	30.2	15.8	14.4	1.10
6243	13.2	5.4	7.8	0.69	31.4	16.3	15.1	1.08
6247	14.6	6.4	8.2	0.78	27.9	14.9	13.0	1.15
6262	14.9	6.3	8.6	0.73	31.3	16.4	14.9	1.10
6268	15.3	7.0	8.3	0.84	30.5	15.3	15.2	1.01
Average	14.3	6.2	8.1	0.77	30.2	15.8	14.4	1.09

TABLE 109

Amblystoma punctatum Series 6212-6281 One-fourth of tail removed

	Living lengths Beginning of experiment April 19 1915						Killed lengths End of experiment June 19 1915			
Catalog number	Total length	Tail length	Body length	$\frac{\text{Tail}}{\text{Body}}$ =	Rem'v'd length	$\frac{\text{Rem'v'd}}{\text{Tail}}$ =	Total length	Tail length	Body length	$\frac{\text{Tail}}{\text{Body}}$ =
6234	14.4	6.2	8.2	0.76	1.7	0.27	32.0	16.8	15.2	1.11
6244	13.6	6.0	7.6	0.79	1.7	0.28	26.9	13.3	13.6	0.98
6249	13.3	5.9	7.4	0.80	1.6	0.27	28.5	14.5	14.0	1.04
6265	15.0	6.5	8.5	0.76	2.0	0.31	27.7	13.3	14.4	0.92
Average	14.1	6.1	7.9	0.78	1.7	0.28	28.8	14.5	14.3	1.01

TABLE 110

Amblystoma punctatum Series 6212-6281 One-half of tail removed

	Living lengths Beginning of experiment April 19 1915						Killed lengths End of experiment June 19 1915			
Catalog number	Total length	Tail length	Body length	$\frac{\text{Tail}}{\text{Body}}$ =	Rem'v'd length	$\frac{\text{Rem'v'd}}{\text{Tail}}$ =	Total length	Tail length	Body length	$\frac{\text{Tail}}{\text{Body}}$ =
6239	14.3	6.3	8.0	0.79	2.8	0.44	28.5	14.5	14.0	1.04
6250	14.3	6.2	8.3	0.75	3.7	0.60	23.1	10.7	12.4	0.86
6255	14.6	6.8	7.8	0.87	3.2	0.47	28.7	14.0	14.7	0.95
6264	15.4	7.2	8.2	0.88	3.5	0.49	24.7	11.5	13.2	0.87
Average	14.7	6.6	8.1	0.81	3.3	0.50	26.2	12.7	13.6	0.93

TABLE 111

Amblystoma punctatum Series 6212-6281 Three fourths of tail removed

	Living lengths Beginning of experiment April 19 1915						Killed lengths End of experiment June 19 1915			
Catalog number	Total length	Tail length	Body length	Tail / Body =	Rem'v'd length	Rem'v'd / Tail =	Total length	Tail length	Body length	Tail / Body =
6216	14.1	6.4	7.7	0.83	4.9	0.77	29.3	14.1	15.2	0.93
6221	13.8	6.1	7.7	0.79	4.3	0.70	16.1	7.0	9.1	0.77
6246	14.1	6.1	8.0	0.76	4.6	0.74	25.5	11.9	13.6	0.87
Average	14.0	6.2	7.8	0.79	4.6	0.74	23.6	11.0	12.6	0.86

TABLE 112

Amblystoma punctatum Series 6212-6231 Summary of averages

	Living lengths Beginning of experiment April 19 1915						Killed lengths End of experiment June 19 1915			
Character of operation	Total length	Tail length	Body length	Tail / Body =	Rem'v'd length	Rem'v'd / Tail =	Total length	Tail length	Body length	Tail / Body =
Control	14.3	6.2	8.1	0.77	——	——	30.2	15.8	14.4	1.09
One-fourth tail...	14.1	6.1	7.9	0.78	1.7	0.28	28.8	14.5	14.3	1.01
One-half tail	14.7	6.6	8.1	0.81	3.3	0.50	26.2	12.7	13.6	0.93
Three-fourts tail.	14.0	6.2	7.8	0.79	4.6	0.74	23.6	11.0	12.6	0.86

BIBLIOGRAPHY

ABEL M.

1902. Beiträge zur Kenntnis der Regenerationsvorgänge bei den limicolen Oligochaeten. Z. f. wiss. zool., 63:1-74.

ALLEN, W. E.

1911. A Study of the Relation of Tissue Differentiation to Rate of Growth during Regeneration. Biol Bull., 21:187-206.

BARFURTH, D.

1903. Die Erscheinungen der Regeneration bei Wirbeltierembryonen. O. Hertwig's Handbuch der Entwickelungslehre der Wirbeltiere.

BONNET, C.

1745. Traité d'insectologie. Seconde partie. Observations sur quelques espèces de vers d'eau douce, qui, coupé par morceaux deviennent autant d'animaux complets. Paris.

DAVENPORT, C. B.

1899. Experimental Morphology, Part II, New York.

DRIESCH, HANS

1897. Studien über das Regulationsvermögen der Organismen, I. Von den regulativen Wachstums-und Differenzirungs-fähigkeiten der Tubularia. Arch. f. Entw. Mech., 5:389-418.

DURBIN, MARION L.

1909. An Analysis of the Rate of Regeneration Throughout the Regenerative Process. J. Exp. Zool., 7:397-420.

ELLIS, M. M.

1909. The Relation of the Amount of Tail Regenerated to the Amount Removed in Tadpoles of Rana clamitans. J. Exp. Zool., 7:421-456.

EMMEL, V. E.

1906. The Relation of Regeneration to the Molting Process in the Lobster. Thirty-sixth Annual Report of the Commissioners of Inland-Fisheries of Rhode Island. Special paper, no. 27:257-313.

KAMMERER, PAUL

1905. Ueber die Abhängigkeit des Regenerationsvermögens der Amphibienlarven von Alter, Entwicklungsstadium und spezifischer Grosze. Arch. f. Entw. Mech., 19:148-180.

KING, HELEN D.

1898. Regeneration in Asterias vulgaris. Arch. f. Entw. Mech., 7:351-363.

MINOT, C. S.

1908. Age, Growth and Death. New York.

Morgan, T. H.
1902. Further Experiments on the Regeneration of the Tail of Fishes. Arch. f. Entw. Mech., 14:539-561.
1906. The Physiology of Regeneration. J. Exp. Zool., 3:457-500.
1909. The Dynamic Factor in Regeneration. Biol. Bull., 16:265-276.
Morgulis, S.
1907. Observations and Experiments on Regeneration in Lumbriculus. J. Exp. Zool., 4:549-574.
1909a. Regeneration in the Brittle-Star Ophiocoma pumila, with Special Reference to the Influence of the Nervous System. Proc. Amer. Acad. of Arts and Sc., 44:655-659.
1909b. Contributions to the Physiology of Regeneration. I. Experiments on Podarke obscura. J. Exp. Zool., 7:595-642.
1909c. Contributions to the Physiology of Regeneration. II. Experiments on Lumbriculus. Arch. f. Entw. Mech., 28:396-439.
Przibram, Hans
1906. Aufzucht, Farbwechsel und Regeneration einer ägyptischen Gottesanbeterin (Sphodromantis bioculata Burm). Arch. f. Entw. Mech., 22: 149-192.
Scott, G. G.
1907. Further Notes on the Regeneration of the Fins of Fundulus heteroclitus. Biol. Bull., 12:385-400.
1909. Regeneration in Fundulus and its Relation to the Size of the Fish. Biol. Bull., 17:343-353.
Spallanzani, Lazaro Abbé
1769. An Essay on Animal Reproductions. Translated by M. Maty. London.
Stockard, C. R.
1908. Studies of Tissue Growth, I. An Experimental Study of the Rate of Regeneration in Cassiopea xamachana. Carnegie Institution Publication No. 103:63-102.
1909a. Studies of Tissue Growth, II. Functional Activity, Form Regulation, Level of the Cut, and Degree of Injury as Factors in Determining the Rate of Regeneration. The Reaction of Regenerating Tissue in the Old Body. J. Exp. Zool., 6:433-471.
1909b. Studies of Tissue Growth, IV. The Influence of Regenerating Tissue on the Animal Body. Arch. f. Entw. Mech., 29:15-32.
Ubisch, Leopold v.
1915. Über den Einflusz von Gleichgewichtsstörungen auf die Regenerationsgeschwindigkeit. Arch. f. Entw. Mech., 41:237-250.
Vanlair, C.
1894. Recherches chronométriques sur la régénération des nerfs. Archives de physiologie normale et pathologique. 5^{e} Série., 6:217-231.
Zeleny, C.
1902. A Case of Compensatory Regulation in the Regeneration of Hydroides dianthus. Arch. f. Entw. Mech., 13:597-609.
1903. A Study of the Rate of Regeneration of the Arms in the Brittle-Star, Ophioglypha lacertosa. Biol. Bull., 6:12-17.

1905a. Compensatory Regulation. J. Exp. Zool., 2:1-102.

1905b. The Relation of the Degree of Injury to the Rate of Regeneration. J. Exp. Zool., 2:347-369.

1907. The Effect of Degree of Injury, Successive Injury and Functional Activity upon Regeneration in the Scyphomedusan, Cassiopea xamachana. J. Exp. Zool., 5:265-273.

1908. Some Internal Factors Concerned with the Regeneration of the Chelae of the Gulf-Weed Crab (Portunus sayi). Carnegie Institution Publication No. 103:103-138.

1909a. The Effect of Successive Removal upon the Rate of Regeneration. J. Exp. Zool., 7:477-512.

1909b. The Relation between Degree of Injury and Rate of Regeneration—Additional Observations and General Discussion. J. Exp. Zool., 7:513-562.

1909c. Some Experiments on the Effect of Age upon the Rate of Regeneration. J. Exp. Zool., 7:563-593.

1912. The Quantitative Study of the Internal Factors Controlling Regeneration. Proc. Seventh Intern. Zool. Congress 1907:491-494.

Zuelzer, M.

1907. Über den Einflusz der Regeneration auf die Wachstumsgeschwindigkeit von Asellus aquaticus. Arch. f. Entw. Mech., 25:361-397.

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THE HEAD-CAPSULE AND MOUTH-PARTS OF DIPTERA

WITH TWENTY-FIVE PLATES

BY

ALVAH PETERSON

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THESIS

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INTRODUCTION

The head and mouth-parts of Diptera offer a rich field for research. A number of excellent studies have been made by several investigators and they deserve careful consideration. A review of practically all the literature shows that a majority of the workers have examined only one or a few species. Meinert (1881) and Hansen (1883), however, studied a number of forms, but they were mostly specialized species; while an important study by Kellogg (1899) deals only with the families of the Nematocera. Becher (1882) is the only investigator who has studied a large series of generalized and specialized species. I have made a special effort to secure as many generalized and specialized species as possible, since it is highly desirable and essential in homologizing structures to have at hand a wide range of species.

Extensive studies have not heretofore been made, so far as I know, on the head-capsule; consequently the important relationship which exists between the mouth-parts and the head-capsule in generalized insects has not been traced in Diptera. This relationship is just as significant in ascertaining the correct interpretation of the mouth-parts of Diptera as it is in other orders. Its importance is illustrated by a study of the head and mouth-parts of the Thysanoptera (Peterson, 1915).

A review of the literature, Dimmock (1881) or Hansen (1883), discloses the many and varied interpretations that have been given to the mouth-parts of Diptera. To arrive at a correct interpretation of the fixed and movable parts of the head, the head-capsule and mouth-parts of all the species studied, irrespective of the established systematic position of the species, have been carefully compared with the head and mouth-parts of generalized insects. On the basis of this comparison, generalized, hypothetical types have been constructed for each fixed and movable part. Each hypothetical type is made up by an accumulation of all the generalized characters found among the Diptera, and should show an intermediate stage between generalized insects and Diptera. The use of such a hypothetical type is a great aid not only in showing how the dipterous type has been developed, but also in determining the homology of the parts.

The scope of this investigation makes it necessary to limit the discussions to the general subject of homology; consequently many details of structure and other interesting modifications, shown in the figures but without direct bearing on the subject of homology, are necessarily disregarded. The fixed and various movable parts of the head are discussed separately, as developed from the hypothetical types, the discussions in every case proceeding from the generalized to the specialized.

All the general conclusions pertaining to the head and mouth-parts presented in the following pages are based entirely on a study of the species listed under "materials", unless otherwise stated. General statements in respect to the mouth-parts are true only for species having them well developed.

The names here adopted for the sclerites of the head and mouth-parts have been made to agree, so far as possible, with the terms now in common use for the same parts in generalized insects. The terms most commonly used thruout the literature for structures peculiar to this order have been adopted unless clearly unsuitable; and new terms have been applied only to structures described here for the first time and to parts to which the current names are inappropriate.

METHODS

The greater part of this study was made from dried specimens that had been soaked from two to twenty-four hours in a 10% solution of potassium hydroxide. The sclerites of weakly chitinized forms show more clearly when they have been soaked for only a short time. After soaking, the heads were washed in distilled water to remove the potassium hydroxide and then preserved in 70% alcohol.

All dissections were made under a binocular microscope in 70% alcohol in deep watch-glasses or in carbol-aniline oil. Studies and figures were largely made from dissected parts in alcohol. Cleared preparations mounted in balsam were also found useful. In making such preparations the parts were dissected, stained, and cleared in carbol-aniline oil. This oil evaporates slowly, will mix readily with safranin or orange G dissolved in 95% alcohol, and will clear from any grade of alcohol above 50%. The staining of material with safranin before mounting proved to be very useful in differentiating the almost colorless parts of some species. When using aniline oil it is necessary to remove as much as possible of the oil before mounting, otherwise the balsam will eventually darken.

The material for sections was fixed with hot (80° C.) corrosive sublimate (saturated corrosive sublimate in 35% alcohol plus 2% of glacial acetic acid) for fifteen minutes to two hours. This was replaced by 70% alcohol containing a few drops of iodine, and the material was allowed to remain in this for twenty-four or more hours. Paraffin having a melting point of 62–64 C. was a sufficiently firm medium in which to cut sections as thin as eight microns. Specimens stained in toto gave the best results. Delafield's haematoxylin required 24–48 hours, and borax carmine 3–7 days.

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MATERIALS

The following list of insects includes all of the identified forms studied. The families of Diptera to which these species belong are arranged according to Aldrich's "Catalogue of North American Diptera". The generic and specific names of all but a few species may likewise be found in this catalog.

Aldrich lists fifty-nine families; of these, one or more representatives of fifty-three families have been studied. The following are not represented: Orphnephilidae, Acanthomeridae, Nemestrinidae, Apioceridae, Rhopalomeridae, and Nycteribiidae. The male and female of each species have been observed except in a few cases; in these the word "male" or "female" after the species name indicates which sex has been seen. Excepting one or two forms, the male and female have both been drawn if they were decidedly different. If the two sexes are similar, the figures were mostly made from the female. An asterisk before the name of a species indicates that this form has been embedded, sectioned, and studied. The figures following the various species refer to the drawings made of the same.

DIPTERA

Suborder Proboscidea

Orthorrhapha-Nemocera.

Tipulidae.—*Tipula bicornis (Fig. 18, 95, 178, 277, 383, 384, 388, and 503), Tipula cunctans, Tipula abdominalis, Limnobia immatura, female (Fig. 93, 386, and 507), Helobia punctipennis, female (Fig. 385), Trichocera bimacula, male (Fig. 16, 78, 158, 200, 260, 311, 365, 499, and 500), Geranomyia canadensis, male (Fig. 382 and 506), Ptychoptera rufocincta (Fig. 15), and Bittacomorpha clavipes, male (Fig. 85 and 389).

Dixidae.—Dixa clavata (Fig. 19, 79, 163, 199, 262, 375, 387, 501, and 502), and Dixa modesta (Fig. 254).

Psychodidae.—Psychoda albipennis (Fig. 8, 82, 166, 202, 263, 318, 372, 529, and 530), and Psychoda sp.

Chironomidae.—Chironomus ferugineovittatus (Fig. 12, 88, 89, 152, 206, 207, 270, 312, 371, 531, and 532), Culicoides sanguisugus (Fig. 253, 265, and 521), and Forcipomyia cilipes.

Culicidae.—Psorophora ciliata (Fig. 10, 26, 96, 159, 210, 211, 251, 266, 373, 380, 381, 504, and 505), Anopheles sp., and *Culex sp.

Mycetophilidae.—Sciara varians (Fig. 17, 81, 150, 205, 267, 314, 360, 512, and 513), Mycetobia divergens (Fig. 7, 90, and 161), Mycetophila punctata (Fig. 11 and 87), and Leia oblectabilis (Fig. 368).

Cecidomyiidae.—Rabdophaga strobiloides (Fig. 6, 86, 170, 201, 268, 313, 367, 510, and 511), and Cecidomyia sp.

Bibionidae.—Bibio femoratus (Fig. 13, 14, 91, 92, 153, 154, 208, 264, 315, 364, 522, and 523), and Bibio albipennis.

Simuliidae.—Simulium venustum, female (Fig. 2, 77, 144, 204, 250, 258, 316, 366, 489, 497, and 498), Simulium johannseni (Fig. 3 and 252), Simulium pecuarum, and Simulium jenningsi.

Blepharoceridae.—Bibiocephala elegantula (Fig. 4, 5, 76, 83, 155, 156, 203, 256, 269, 399, 526, and 527), and Blepharocera sp.

Rhyphidae.—Rhyphus punctatus (Fig. 9, 80, 157, 209, 261, 321, 374, 508, and 509).

Orthorrhapha-Brachycera.

Stratiomyiidae.—Stratiomyia apicula (Fig. 27, 28, 104, 160, 213, 273, 331, 395, 396, 545, and 546), and Stratiomyia meigeni.

Tabanidae.—Tabanus giganteus (Fig. 20, 21, 74, 75, 142, 143, 214, 255, 259, 283, 317, 390–392, and 494–496), Tabanus sulcifrons, Tabanus atratus, Tabanus trimaculata, and Chrysops striatus.

Leptidae.—Leptis vertebrata (Fig. 34, 35, 103, 145, 218, 275, 323, 369, 370, 520, and 525), Chrysopila proxima, Chrysopila thoracica, Chrysopila quadrata, and Chrysopila velutina.

Cyrtidae.—Oncodes costatus (Fig. 53, 105, 109, 220, 486, and 487), Eulonchus tristis (Fig. 284a, 364a, 425a, 425b, and 543), and Pterodontia flavipes.

Bombyliidae.—Exoprosopa fasciata (Fig. 29, 98, 162, 216, 285, 361-426–429, 549, and 550), Systoechus vulgaris, Lepidophora sp., and Bombylius major (Fig. 482).

Therevidae.—Psilocephala haemorrhoidalis (Fig. 33, 36, 100, 173, 281, 324, 402, 403, 533, and 534).

Scenopinidae.—Scenopinus fenestralis (Fig. 41, 42, 107, 149, 219, 282, 325, 400, 401, 537, and 538).

Mydaidae.—Mydas clavatus (Fig. 30, 99, 146, 212, 271, 319, 397, 398, 535, and 536).

Asilidae.—Promachus vertebratus (Fig. 22, 84, 147, 148, 217, 276, 322, 376–379, and 517–519), Asilus notatus, and Deromyia umbrina.

Dolichopodidae.—Dolichopus bifractus (Fig. 43, 112, 168, 226, 284, 432–434, 524, and 528), Dolichopus sp. (Fig. 108), Psilopodinus sipho, and Sympycnus lineatus.

Empididae.—*Empis clausa (Fig. 26, 40, 97, 164, 215, 274, 352, 421–423, 547, and 548), Rhamphomyia glabra (Fig. 424 and 425), and Euhybus sp.

Lonchopteridae.—Lonchoptera lutea (Fig. 37, 102, 177, 223, 280, 320, 406–408, 539, and 541).

Phoridae.—Aphiochaeta agarici (Fig. 31, 111, 174, 224, 278, 335, 393, 394, 540, and 544), Metopina sp., and Dohrniphora concinna.

Cyclorrhapha-Athericera.

Platypezidae.—Platypeza velutina (Fig. 32, 110, 165, 222, 272, 326, 415, 416, 542, and 542a).

Pipunculidae.—Pipunculus cingulatus (Fig. 38, 39, 106, 151, 243, 279, 327, 435, 436, 561, and 562).

Syrphidae.—Eristalis tenax (Fig. 23–25, 113, 167, 232, 286, 328, 441–443, 587, and 588), Syritta pipiens, and *Allograpta obliqua.

Conopidae.—Conops brachyrhynchus (Fig. 67, 117, 186, 221, 305, 356, 417–420, 591, and 592), Stylogaster biannulata (Fig. 359), and Physocephala tibialis.

Cyclorrhapha-Calyptratae.

Oestridae.—Gastrophilus equi (Fig. 54, 138, 239, and 490–492).

Tachinidae.—Archytas analis (Fig. 68, 124, 197, 247, 309, 353, 468, 469, 604, and 605), Siphona geniculata (Fig. 355 and 458), Gonia capitata, Ocyptera carolinae, and Gymnosoma fuliginosa.

Dexiidae.—Thelaira leucozona (Fig. 65, 128, 196, 230, 301, 346, 473, 474, 595, and 596).

Sarcophagidae.—Sarcophaga haemorrhoidalis (Fig. 66, 130, 191, 244, 310, 350, 477, 478, 602, and 603).

Muscidae.—*Musca domestica (Fig. 71, 72, 133, 194, 242, 304, 351, 465–467, 600, and 601), Calliphora vomitoria (Fig. 484 and 485), *Stomoxys calcitrans (Fig. 354, 479, 480, and 599), Myiospila meditabunda (Fig. 120), Pollenia rudis, Lucilia caesar, and Calliphora erythrocephala.

Anthomyiidae.—Hydrotaea dentipes (Fig. 69, 70, 127, 195, 241, 308, 349, 475, 476, 597, and 598), Lispa nasoni (Fig. 116 and 481), Dexiopsis lacteipennis, Coenosia aurifrons, and Chortophila sp.

Cyclorrhapha-Acalyptratae.

Scatophagidae.—Scatophaga furcata (Fig. 62, 135, 193, 246, 307, 357, 470–472, 593, and 594).

Heteroneuridae.—Heteroneura flaviseta (Fig. 49, 126, 176, 229, 298, 340, 459, 460, 589, and 590).

Helomyzidae.—Oecothea fenestralis (Fig. 48, 137, 192, 227, 290, 332, 452, 453, 580, and 581).

Borboridae.—Borborus equinus (Fig. 63, 136, 188, 231, 294, 342, 437, 438, and 565–567), Limosina ferruginata, and Sphaerocera pusilla.

Phycodromidae.—Coelopa vanduzeii (Fig. 58, 121, 182, 288, 337, 448, 449, 559, and 560).

Sciomyzidae.—Tetanocera plumosa (Fig. 55, 119, 180, 225, 302, 344, 463, 464, 584, and 586), and Sepedon fuscipennis.

Sapromyzidae.—Sapromyza vulgaris (Fig. 60, 115, 171, 248, 289, 329, 409, 410, 553, and 554), Sapromyza bispina, Minettia lupulina, and Lonchaea polita.

Ortalididae.—Chrysomyza demandata (Fig. 64, 134, 181, 245, 295, 341, 456, 457, 557, and 558), Tritoxa incurva, Chaetopsis aenea, Camptoneura picta, Pyrgota sp., and Eumetopia sp.

Trypetidae.—Euaresta aequalis (Fig. 61, 131, 175, 240, 292, 347, 413, 414, 572, and 573), Trypeta alba, and Straussia longipennis.

Micropezidae.—Calobata univitta (Fig. 44, 114, 183, 236, 296, 348, 446, 447, 551, and 552).

Sepsidae.—Sepsis violacea (Fig. 46, 118, 184, 234, 287, 334, 439, 440, 582, and 583), and Prochyliza xanthostoma.

Psilidae.—Loxocera pectoralis (Fig. 59, 123, 169, 235, 300, 339, 461, 462, 570, and 571).

Diopsidae.—Sphyracephala bicornis (Fig. 52, 94, 190, 293, 338, 450, 451, and 585).

Ephydridae.—Ochthera mantis (Fig. 56, 101, 187, 237, 297, 336, 444, 445, 483, and 574–577), Paralimna appendiculata, and Parydra bituberculata.

Oscinidae.—Chloropisca glabra (Fig. 51, 132, 189, 306, 345, 430, 431, 555, and 556), Siphonella abdominalis, and Hippelates flavipes.

Drosophilidae.—Drosophila ampelophila (Fig. 45, 125, 172, 238, 291, 343, 454, 455, 563, and 564).

Geomyzidae.—Chyromya concolor (Fig. 50, 122, 179, 233, 299, 333, 411, 412, 568, and 569).

Agromyzidae.—Desmometopa latipes (Fig. 47, 129, 185, 228, 303, 330, 404, 405, 578, and 579).

Suborder Eproboscidea

Hippoboscidae.—Olfersia ardeae (Fig. 57, 139, 198, 249, 358, 488, and 606), and Melophagus ovinus.

ORTHOPTERA

Periplaneta orientalis (Fig. 514).
Melanoplus differentialis (Fig. 515).
Gryllus pennsylvanicus (Fig. 516).

Hypothetical and typical figures (Fig. 1, 73, 140, 141, 199h, 256h, 257, 362, 363, and 493).

FIXED PARTS OF THE HEAD

A hypothetical head-capsule of Diptera (Fig. 1) has a dorso-ventral extension. The epicranial suture (e. s) is present on the meson, and extends from the occipital foramen (o. f) to a point on the cephalic aspect ventrad of the antennae. At this point it bifurcates and the two arms continue to the invaginations of the anterior arms of the tentorium (i. a), which are situated at the dorso-lateral angles of the clypeus (c). The three unpaired sclerites included within, or ventrad of, the fork of the epicranial suture are the front (fr), clypeus (c), and labrum (l). The fronto-clypeal suture is represented by a dotted line in the figure. The vertex (v) includes all of the dorsal and cephalic aspects of the epicranium except the front (fr), while the genae (ge) are the regions of the vertex ventrad and mesad of the compound eyes. Two large compound eyes (c. e) cover the lateral portions of the cephalic aspect. Three ocelli (oc) are situated on the vertex. The occiput (occ) and postgenae (po) constitute the caudal aspect of the head-capsule.

The tentorium (t) of the hypothetical head-capsule has three pairs of invaginations, homologous with the invaginations in generalized insects. The invaginations of the posterior arms (i.p) of the tentorium are situated ventrad of the occipital foramen at the distal ends of chitinized thickenings. The invaginations of the dorsal arms of the tentorium (i.d) are on the cephalic aspect near the antennae and adjacent to the epicranial suture, while the invaginations of the anterior arms of the tentorium (i.a) are situated in the epicranial suture and adjacent to the dorso-lateral angles of the clypeus.

The heads of all Diptera have a dorso-ventral extension, and in this respect resemble the heads of many generalized insects. Some of the primary sutures, sclerites, and invaginations of the head of such an insect are present in a number of the Nematocera and in a few of the Brachycera. The hypothetical head-capsule has been constructed from these forms. The heads of the Acalyptratae and the Calyptratae are highly specialized by the modification, union, reduction, and membranous development of parts, consequently very few if any primary characters remain which can be homologized with these structures. The membranous development of areas has been the most important process of specialization. The stippled areas on the figures show the extent of the membrane. The various parts of the head-capsule are discussed individually and in the order in which they were described for the hypothetical type. The heads of Diptera naturally fall into two groups according to the presence or absence of a frontal suture (fr.s) and a ptilinum (pt). The forms without a frontal suture are the more generalized.

Epicranial Suture.—The epicranial suture of all insects originates in the embryo. The stem of the suture on the dorso-meson represents the line along which the paired parts of the head meet, while the arms of the suture (a. e. s) represent the place of contact between the paired sclerites of the head and the mesal unpaired sclerites. The epicranial suture (e. s) of a hypothetical dipterous head corresponds to the above description, and is homologous with the epicranial suture found in the heads of generalized immature and adult insects of the more common orders. The following examples illustrate the homology between the hypothetical type and other insects. The epicranial suture in the larva of Corydalis, and in the generalized larvae of the Coleoptera, Lepidoptera, and certain Hymenoptera, is complete, and its two arms join with the margins of the clypeus, as in the hypothetical type.

The epicranial suture of the adults of the Orthoptera, Hemiptera, and Hymenoptera also resembles this suture in the hypothetical head, providing the following interpretation of this suture is accepted. In the adults of Gryllus and Periplaneta it is complete and similar to that of Corydalis except that a small portion of each arm is wanting about the antennae and the lateral ocelli. The ventral ends of the arms are commonly called the fronto-genal sutures, and they join with the clypeus as in Corydalis. All insects that have a sucking type of mouth, such as the Hemiptera and Hymenoptera, usually show no signs of the stem of the epicranial suture. The arms, however, are distinct and form the lateral and dorsal boundaries of the large mesal piece commonly called the clypeus. A large number of the Diptera possess an epicranial suture which closely resembles that of the Hemiptera and the Hymenoptera. On the basis of the above interpretation of the epicranial suture it has been possible to homologize the sutures and sclerites, and the invaginations of the tentorium on the cephalic aspect. No other interpretation gave satisfactory results.

The epicranial suture (e. s) in Mycetophila (Fig. 11) is complete and closely resembles the hypothetical type. In Leia it closely resembles that of Mycetophila except for the stem of the suture, which is wanting dorsad of the median ocellus. The stem of the epicranial suture in Psorophora (Fig. 10 and 26) and Chironomus (Fig. 12) is represented by a distinct suture in a deep fold on the meson. Other forms, such as Rhabdophaga (Fig. 6), Mycetobia (Fig. 7), and Tabanus (Fig. 20), show depressions or thickenings along the meson. These marks may have no significance. Outside of the above-mentioned forms, the stem of the epicranial suture is wanting.

The arms of the epicranial suture (a. e. s) are present in many Diptera. This is the case in all but a few of the Nematocera, in a majority of the Brachycera, and in many of the families of the Cyclorrhapha. These resemble, therefore, the adults of the Hemiptera and Hymenoptera. The arms are present as definite sutures between two chitinized areas in Tabanus (Fig. 20 and 21) and Leptis (Fig. 35), and in the female of Simulium (Fig. 2). The epicranial suture is apparently wanting in the male of Simulium (Fig. 3) unless the lateral margins of the convex area represent it. In many genera the epicranial suture is represented by the edge of a chitinized sclerite. This is the case in Chironomus (Fig. 12), Trichocera (Fig. 16), Psorophora (Fig. 10), Mycetobia (Fig. 7), and Dixa (Fig. 19). The vertex in the genera just named is membranous between the antennal fossae and the epicranial suture. Sciara (Fig. 17), Rhabdophaga (Fig. 6), Bibiocephala (Fig. 4 and 5), and possibly Rhyphus (Fig. 9) and Bibio (Fig. 14), have the arms of the epicranial suture represented by the chitinized margin of the vertex, which is adjacent to the membranous portion of the fronto-clypeus. The location of the invaginations of the arms of the tentorium usually helps to determine the location of the epicranial suture. In Ptychoptera (Fig. 15) the invaginations of the anterior arms of the tentorium are located in the distinct V-shaped depression on the chitinized area ventrad of the antennae. Undoubtedly this depression marks the position of the epicranial suture. Tipula (Fig. 18) has a very specialized head and shows no epicranial suture or tentorium.

Only the arms of the epicranial sutures are present in the Brachycera. On the whole these sutures are not as well developed in the Brachycera as in the Nematocera. When present (a. e. s) they are long and slit-like in all the genera except Tabanus. This condition is due to the fusion of the invaginations of the dorsal arms and the anterior arms of the tentorium along each suture. The arms of this suture in Tabanus (Fig. 20 and 21) unite the invaginations on each lateral half of the head, but they are not decidedly slit-like.

The arms of the epicranial suture (a. e. s) in Tabanus (Fig. 20) have the usual inverted-u shape and their ventral ends terminate at the ventral margin of the head. The arms are indistinct ventrad of the invaginations of the anterior arms of the tentorium. The invaginations (i. a) in Promachus (Fig. 22) are slit-like and situated near the ventro-lateral angles of the compound eyes. The epicranial suture is wanting dorsad and ventrad of the invaginations of the anterior arms, and in this respect Promachus differs from Leptis and Tabanus. From Leptis (Fig. 35) it is possible to homologize the arms of the epicranial suture of all the Brachycera and those of the Cyclorrhapha. The arms of the suture in Leptis are long and slit-like and coincide with the invaginations of the tentorium on the cephalic aspect of the head. They extend dorsad from the ventral margin of the head to a point ventrad of the antennae, where they unite and enclose a convex mesal area called the fronto-clypeus (fr. c). This suture (a. e. s) in Platypeza (Fig. 32) closely resembles that of Leptis. The dorsal ends of the arms of the epicranial suture are wanting in Psilocephala (Fig. 36), Mydas (Fig. 30), Exoprosopa (Fig. 29), Eristalis (Fig. 23 and 25), and Scenopinus (Fig. 41 and 42), and in other forms. Scenopinus shows a striking variation in that the vertex is membranous between the antennae and the fronto-clypeus, and no epicranial suture can be traced thru the membrane. Stratiomyia (Fig. 27) shows a unique development of the slits in that they extend mesad rather than dorsad. This condition is undoubtedly a secondary development. The epicranial suture of Lonchoptera, Aphiochaeta, Pipunculus, and Empis is discussed under fronto-clypeus.

No epicranial suture or slit-like invaginations are present in any dipteron that has a frontal suture (fr. s) or a ptilinum (pt). Since the tentorium on the cephalic aspect and the arms of the epicranial suture are usually closely associated in insects, there is every reason to believe that the tentorial thickenings (t. th) mark the course of the suture (a. e. s). Furthermore, the location of the thickenings of the tentorium is very similar to the location of the slit-like invaginations of Leptis (Fig. 35). These thickenings (t. th) have been considered as marking the course of the arms of the epicranial suture. The extent of the tentorial thickenings varies considerably, as shown in the figures. In Tetanocera (Fig. 55), Chloropisca (Fig. 51), Heteroneura (Fig. 49), and others, the tentorial thickenings extend to the antennal fossae (a. f). No sutures are present between the dorsal ends of these thickenings.

Fronto-clypeus.—The front (fr) and clypeus (c) of all insects are unpaired sclerites located between the arms of the epicranial suture (a. e. s). The labrum (1) is also an unpaired sclerite attached typically to the ventral margin of the clypeus. These three sclerites and their parts are not always distinguishable. This is particularly true of the front and clypeus in Diptera. The dotted, transverse line uniting the invaginations of the anterior arms of the tentorium (i. a) in the hypothetical head indicates the position of the fronto-clypeal suture. In a few of the Orthorrhapha, suture-like marks, depressions, or thickenings extend across the chitinized portion of the fronto-clypeus. These marks in Chironomus (Fig. 12), Mycetophila (Fig. 11), and Rhabdophaga (Fig. 6) resemble the fronto-clypeal suture as indicated in the hypothetical type. It is possible that they are remnants of this suture. Excepting in the forms named, one can not be sure of the presence of a fronto-clypeal suture; consequently the entire area between the labrum and the arms of the epicranial suture has been designated as the fronto-clypeus (fr. c). The absence of the fronto-clypeal suture in Diptera is not unusual, since it is wanting in many generalized insects. For those who may wish to divide the fronto-clypeus into two areas, the dorsal half would be the front and the ventral half the clypeus. A large portion of the fronto-clypeus is membranous in Rhabdophaga (Fig. 6), Rhyphus (Fig. 9), and Sciara (Fig. 17), and the chitinized part is greatly reduced. The variations found in the Nematocera are represented in the figures.

The Brachycera show two lines of development in the modification of the area enclosed by the arms of the epicranial suture. Both of these started from a form which possessed an epicranial suture similar to that of Leptis (Fig. 35). The line of development seen in Psilocephala, Platypeza, Scenopinus, Lonchoptera, and Aphiochaeta is considered first. The chitinized fronto-clypeus of Leptis resembles the fronto-clypeus of a number of the Nematocera, as Sciara (Fig. 17). From this simple condition it is possible to develop the type of fronto-clypeus found in Psilocephala (Fig. 33 and 36). This came about by a membranous development on the meson and on the lateral margins of the fronto-clypeus and the loss of the arms of the epicranial suture directly ventrad of the antennae. The membranous development of the fronto-clypeus of Platypeza (Fig. 32) resembles that of Psilocephala. Scenopinus (Fig. 41 and 42) belongs to this same line, but in this genus the antennae are adjacent to the fronto-clypeus and no portion of the chitinized vertex exists between them. The form of the chitinized portion of the fronto-clypeus resembles closely that of Platypeza (Fig. 32). Aphiochaeta (Fig. 31) and Lonchoptera (Fig. 37) apparently belong to this same series. If such is the case, the arms of the epicranial suture do not project dorsad but are represented by the nearly straight ventral margin of the cephalic aspect. This condition must have come about by the straightening out of the usual u-shaped depression, and the chitinized part of the fronto-clypeus is located ventrad of the margin of the head. The tentorial thickenings along the ventral margin of the head in Lonchoptera afford evidence favorable to the above interpretation. A similar type of development occurs in Bibio (Fig. 14), in which the invaginations for the anterior arms of the tentorium are located on the ventral margin of the head-capsule latero-ventrad of the antennal fossae. All the other Brachycera and Cyclorrhapha figured, show the presence of sclerites designated as the tormae and located ventrad of the fronto-clypeus, and this fact places them in the line of specialization which leads toward a muscid type.

The fronto-clypeus (fr. c) is present in all Diptera and constitutes a prominent portion of the head-capsule. In Tabanus (Fig. 20 and 21) the fronto-clypeus is the entire area ventrad of the epicranial suture and outside of the tormae and the labrum. The sutures separating the fronto-clypeus from the genae (ge) are very indistinct. No arms of the epicranial suture are present in Promachus (Fig. 22), Empis (Fig. 40), and Pipunculus (Fig. 38); consequently the dorsal extent of the fronto-clypeus can not be determined, and the area ventrad of the antennae is considered as the fronto-clypeus. The fronto-clypeus of Mydas (Fig. 30) resembles that of Leptis, and from a type similar to Mydas it is possible to develop the fronto-clypeus of Exoprosopa (Fig. 29), Eristalis (Fig. 25), and probably Stratiomyia (Fig. 27). The fronto-clypeus of Mydas closely resembles that of the Acalyptratae and the Calyptratae, as will be seen by comparing Mydas with Tetanocera (Fig. 55), Chloropisca (Fig. 51), Chyromya (Fig. 50), and Musca (Fig. 72). It is not a completely chitinized area in all of the genera studied, and the significance of this mesal membranous area in Sepsis, Oecothea, and Calobata has been suggested in the discussion on the ptilinum.

Tormae.—The tormae (to) in generalized insects are chitinized pieces which belong to the lateral portions of the epipharynx in the region of the clypeo-labral suture and connect with the clypeus or labrum at the lateral ends of the suture. These are well illustrated in such Orthoptera as Periplaneta (Fig. 514), Melanoplus (Fig. 515), and Gryllus (Fig. 516).

The tormae of generalized Diptera also connect with the inner surface of the ventral portion of the fronto-clypeus. They are not well-developed structures or readily distinguishable from the fronto-clypeus in a number of species of the Nematocera. This seems to be due to the decidedly convex nature of the fronto-clypeus and the close proximity of its lateral portions to the lateral margins of the epipharynx. The tormae of Leptis (Fig. 520), Psilocephala (Fig. 36 and 533), Scenopinus (Fig. 41 and 538), Aphiochaeta (Fig. 31 and 544) Lonchoptera (Fig. 37 and 539), and Platypeza (Fig. 32 and 543) connect with the fronto-clypeus and thus resemble the Nematocera and the hypothetical type. In Tabanus, the tormae (Fig. 494) resemble the above genera in their connection with the fronto-clypeus, but they have been enlarged ventrad until they are exposed between the clypeus and the labrum (Fig. 20 and 494). The exposed portions of the tormae resemble two small, triangular sclerites with their pointed ends meeting on the meson. This condition is not unusual since they resemble closely the exposed portions of the tormae located at the lateral ends of the clypeo-labral suture in Gryllus (Fig. 516). Simulium (Fig. 2 and 489) also shows exposed portions of the tormae at the ventro-lateral angles of the fronto-clypeus (fr. c).

The inverted chitinized V-shaped piece ventrad of the fronto-clypeus in Mydas (Fig. 30) has undoubtedly been derived from the fusion of the tormae of some form resembling Tabanus (Fig. 20). The tormae are adjacent to the fronto-clypeus in Mydas, but they are not connected with the same as in Tabanus. From the type of tormae found in Mydas it is possible to develop the tormae of all other genera. The tormae vary in shape and position as seen in the cephalic views of the head. In Exoprosopa (Fig. 29), Eristalis (Fig. 25), and Stratiomyia (Fig. 27) they show a striking development in that they are located within deep emarginations of the ventral margin of the fronto-clypeus. The tormae of Empis (Fig. 40) closely resemble those of Mydas and belong to the same line of development. In Pipunculus (Fig. 38) the tormae resemble the fronto-clypeus of Sciara (Fig. 17), but as a matter of fact the fronto-clypeus is the area ventrad of the antennae, as shown by the location (Fig. 151) of the dorsal arms of the tentorium (d. a). The tormae of the Acalyptratae are usually crescent-shape, while in the Calyptratae they resemble the type found in Mydas.

Ptilinum.—A deep, inverted U-shaped groove is present in the heads of all the Calyptratae and the Acalyptratae dorsad of the antennae. This groove is called the frontal suture (fr. s) and marks the line of invagination of the large membranous pouch, the ptilinum (pt). In Sphyracephala (Fig. 52) the frontal suture is V-shaped, owing to the peculiar development of the head. The extent of the invagination of the ptilinum (pt) is indicated by a dot-and-dash line in the drawings of the cephalic and lateral views of the head-capsule.

The origin of the ptilinum has been a mystery to morphologists. After a careful examination of the heads of the Brachycera and the Cyclorrhapha, no definite data were found which would throw any light on its origin. A few forms, however, suggested a possible way in which it might have been developed. The frontal suture and the ptilinum are comparatively small in Tetanocera (Fig. 55), Sapromyza (Fig. 60), Conops (Fig. 67), Ochthera (Fig. 56), and Chloropisca (Fig. 51). These genera gave no clue to the early stages of its development unless the thinly chitinized condition of the fronto-clypeus of Chloropisca has some significance. It seems evident that the frontal suture was once a membranous area which became invaginated to form a membranous pouch or ptilinum. If this is the case, the mesal membranous area of the fronto-clypeus of Sepsis (Fig. 46), Oecothea (Fig. 48), Calobata (Fig. 44), and Desmometopa (Fig. 47) would be very significant. The ptilinum might possibly have originated from some form similar to Scenopinus (Fig. 41), in which the ventral margin of the chitinized vertex is located dorsad and laterad of the antennae. It seems quite possible that the membrane along this margin became invaginated in the early stages of the development of the ptilinum. The above conjectures may or may not be correct. A real solution of the problem will undoubtedly require a careful study of the pupal development.

Labrum.—The labrum (l) of a hypothetical dipterous head (Fig. 1, 140, and 493) is a distinct, chitinized, tongue-like structure connected with the ventral margin of the clypeus. The shape and size of the labrum are identical with the shape and size of the epipharynx, which is located on its caudal aspect. The labrum (l) and epipharynx (ep) are joined together by a membrane along their lateral margins. These two structures thus act as one organ and they have rightly been called the labrum-epipharynx (l. ep). The above relation of the labrum to the epipharynx and the fronto-clypeus resembles that in the Orthoptera.

In a general way the labrum of all the genera studied resembles the hypothetical type described above. It varies, however, in shape and in degree of chitinization. In Promachus (Fig. 22), in Psorophora (Fig. 10 and 26), and in the female of Tabanus (Fig. 20) it is completely chitinized and separated from the fronto-clypeus by a suture. In all other genera there is a distinct membranous area present between the fronto-clypeus and the labrum. This area is very extensive in the Cyclorrhapha and includes the ectal exposure of the tormae. The labrum of a few scattered genera, such as Rhabdophaga (Fig. 6), Mycetobia (Fig. 7), Chironomus (Fig. 12), Scenopinus (Fig. 41), and others, is completely membranous, while in still others it is nearly so, as in Mydas (Fig. 30). The figures of the cephalic aspect of the head and the lateral views of the epipharynx and the hypopharynx show the shape and extent of the chitinization of the labrum.

The labrum of Dixa (Fig. 501), Trichocera (Fig. 499), Sciara (Fig. 513), Bibio (Fig. 523), Simulium (Fig. 497), Culicoides (Fig. 521), Tabanus (Fig. 20), and Dolichopus (Fig. 528) is distinctly separated from the epipharynx (ep) by a membrane. This condition is best seen in a lateral view. A majority of the forms studied have little or no membrane between the labrum and epipharynx. This is particularly true of the Cyclorrhapha. The surface of the labrum of all Diptera is more or less convex. In a large number of the genera the convexity is very decided and of such a nature as to surround the cephalic and lateral aspects of the epipharynx. The epipharynx in these forms can only be seen in a caudal view. In the Calyptratae, the labrum and epipharynx are firmly united in one piece.

The labrum of Simulium (Fig. 2 and 489) is unique in that the chitinized part consists of a narrow mesal piece which bifurcates at its distal end. These bifurcations give rise to special small hook-like structures (h) which have been incorrectly interpreted as mandibles (Smith, 1890). The labrum and epipharynx of Psorophora (Fig. 504) fit together very closely. By careful dissection they may be separated, as seen in the drawing. So far as observed, no membrane is present between them. The proximal end of the labrum is crook-like in form, and muscles connect with this portion.

Vertex.—The vertex (v) of a hypothetical head (Fig. 1) consists of the paired continuous areas on the cephalic aspect of the epicranium. It is interpreted as including all the cephalic and dorsal aspects of the epicranium except the front. In a number of the Diptera, as heretofore described, the stem of the epicranial suture (s. e. s) is present and marks the line of fusion of the two halves of the vertex, upon which the ocelli and the antennae are located. The shape and size of the chitinized portion of the vertex is largely determined by the size of the compound eyes, the location and extent of the membranous area about the base of the antennae, and the location of the arms of the epicranial suture. The variations in the size and shape of the vertex are shown in the figures of the cephalic aspect of the head.

The region of the vertex ventrad and mesad of each compound eye is a gena. The size of the genae (ge) is dependent upon the location of the compound eyes and the ventral extension of the head-capsule. The figures show considerable variation in these respects.

Compound Eyes and Ocelli.—The compound eyes (c. e) of a hypothetical head are large oval structures located on the cephalo-lateral aspects of the head-capsule. They cover from one-half to two-thirds of the entire cephalic aspect and their caudal margins are adjacent to the lateral margins of the head. The compound eyes of a majority of the Diptera resemble in general the hypothetical type. The shape and size vary considerably with the different species. Variations are most prevalent in the families of the Orthorrhapha. This variability agrees with the decided variability of other parts. In such genera as Tipula (Fig. 95), Psorophora (Fig. 96), and Limnobia (Fig. 93) the compound eyes are exceptional in that they extend onto the caudal aspect of the head. The variations in shape are well illustrated by the numerous figures.

The compound eyes show secondary characters in a greater number of species than any other fixed or movable part. This sexual variation is most prevalent among the Nematocera and the Brachycera, and was not observed in the Acalyptratae. Among the Calyptratae, slight differences occur in Musca (Fig. 71 and 72) and Hydrotaea (Fig. 69 and 70). When sexual variation occurs, the eyes of the male are larger than those of the female, and they are usually adjacent along a portion of their mesal margins. Such species are said to be holoptic; while all the females, and some of the males, having the eyes distinctly separated, are dichoptic. The extent of the holoptic condition depends upon the size of the eyes and the location of the antennal fossae, as in Simulium (Fig. 2 and 3) and Bibio (Fig. 13 and 14). In the male of Bibio the compound eyes are adjacent along their mesal margin and the antennal fossae (a. f) are located ventrad of the eyes. The extent and nature of the sexual variation is shown in the figures. Except in the case of Empis the heads of the male and female have both been drawn when decided differences are present.

The facets or ommatidia of the compound eyes vary in number, form, and size thruout the order. In the Nematocera they are usually large and not as closely compacted as in the Cyclorrhapha. An interesting variation occurs in the male of Simulium, the facets (fa) of the ventral half of the eye being smaller than those of the dorsal half. This difference is also found in the female of Bibiocephala (Fig. 5). In the male of Bibio (Fig. 154) the facets (fa) in the ventro-caudal portions of the eyes are smaller than the others. The compound eyes of Bibiocephala and Blepharocera are divided into a dorsal and a ventral portion by a transverse constriction (ch), where the ommatidia are wanting. This constriction is also present in Bibio, but in this form it is confined to the caudo-ventral portion of the eye.

The drawings of the lateral aspects of some heads show a line of dashes or a solid line around the margins of the compound eyes. This line indicates the extent of the infolding of the head-capsule adjacent to the compound eye. This infolding, or ocular sclerite (o. s), is figured only for those species in which it is closely related to the external markings found on the caudal aspect dorsad of the occipital foramen. The influence of this invaginated edge will be more fully discussed later.

The three ocelli (oc) of the hypothetical head-capsule (Fig. 1) are arranged in the form of a triangle and located on the cephalo-dorsal aspect of the vertex. The median ocellus is in the epicranial suture, somewhat ventrad of the lateral ocelli. In Leia it is in this suture somewhat dorsad of the bifurcation, and the other two ocelli are somewhat laterad of it. This location of the ocelli in the Diptera agrees with Comstock's idea concerning the caudal migration of the ocelli in specialized insects. In generalized insects all three ocelli may be on the front or two on the vertex while the median ocellus is on the front. The ocelli in the Hymenoptera and Hemiptera are similar in location to those of the Diptera.

Leia is the only form studied which has ocelli and a well-marked stem of the epicranial suture. The chitinized, secondary, Y-shaped thickenings on the ocellar triangle of Rhyphus (Fig. 9) and Mycetobia (Fig. 7) should not be confused with the epicranial suture. Three ocelli are present in all other genera of Diptera examined except Oncodes (Fig. 53) and Mycetophila, in which there are only two. The median ocellus is wanting in Mycetophila, while the lateral ocelli are small inconspicuous bodies, adjacent to the dorso-mesal margin of the compound eyes (not shown in the figure). The figures show such variations as occur in the various ocellar groups.

Occiput and Postgenae.—No sutures occur on the caudal aspect of the hypothetical head-capsule (Fig. 73) except the epicranial suture (e. s). This absence of sutures makes it impossible to locate definitely the boundaries of the occiput and the postgenae. The following interpretation is based upon a study of the occiput and postgenae of generalized insects, such as the Orthoptera. The occiput comprises all the area dorsad of an imaginary transverse line drawn thru the middle of the centrally located occipital foramen. The areas ventrad of this line and laterad of the mesal membranous areas are the postgenae. The occiput (occ) undergoes a secondary development about the margin of the occipital foramen. The structures pertaining to this modification have been designated as the parocciput (pocc). Each postgena (po) is also secondarily differentiated along its mesal margin by a chitinized thickening which extends between the occipital foramen and the invaginations of the posterior arms of the tentorium. This thickening has been designated as the parapostgenal thickening, while the area mesad of it is the parapostgena (ppo). The two mesal projections of the parocciput on the lateral margin of the occipital foramen serve as points for the articulation of neck sclerites and mark the ventral boundary of the occiput.

The occipital foramen (o. f) is centrally situated in all but a few genera, such as Tipula (Fig. 95), Limnobia (Fig. 93), Psorophora (Fig. 96), and Bibio (Fig. 92), in which it is near the dorsal margin. The size of the occipital foramen is more or less constant thruout the order, but in Psychoda (Fig. 82) and Promachus (Fig. 84) it is comparatively much larger than in Pipunculus (Fig. 106) and Exoprosopa (Fig. 98). The shape of the occipital foramen varies somewhat, but usually it is in the form of a figure eight. The constrictions in the lateral margins are generally due to the mesal projections of the parocciput, which vary to some extent in their situation. The projections in Exoprosopa (Fig. 98), Pipunculus (Fig. 106), and Mydas (Fig. 99) meet on the meson and completely divide the occipital foramen into two openings. The neck sclerites (n. s) always articulate with these mesal projections and are represented in a number of the figures.

The occiput (occ) of all genera figured resembles in general the occiput of the hypothetical head, since no sutures separate the vertex, the occiput, and the postgenae. The position of the occipital foramen and the contour of the caudal surface determine the amount of variation in the occiput as well as in the postgenae. In some genera, Empis (Fig. 164) and Bibiocephala (Fig. 156), the caudal aspect is convex; while in others, Exoprosopa (Fig. 98) and Pipunculus (Fig. 106), it is decidedly concave. Suture-like markings or depressions are present near the dorsal margin of the caudal aspect in the heads of Tabanus (Fig. 74), Stratiomyia (Fig. 104), Bibio (Fig. 91), Bibiocephala (Fig. 83), Leptis (Fig. 103), Psilocephala (Fig. 100), and others. These depressions mark the place of contact of the mesal portions of the ocular sclerites with the head-capsule, and are in no way homologous with the sutures about the occiput in generalized insects.

The area about the dorsal and lateral margin of the occipital foramen, the parocciput (pocc), is more or less differentiated from the remainder of the occiput in all the species studied. In the more generalized forms, Bibiocephala (Fig. 83), Trichocera (Fig. 78), Tipula (Fig. 95), Sciara (Fig. 81), and Bittacomorpha (Fig. 85), it is only a thickened edge; but in a large number of species thruout the order it is a clearly defined piece, set off from the occiput proper by a secondary suture. The indefiniteness of this piece in a large number of the generalized Diptera and the want of an homologous part in generalized insects support the view that it is only a secondary modification of the occiput.

The parocciput (pocc). in most genera, occurs as a narrow piece about the dorsal and lateral margin of the occipital foramen, and its ventral ends project mesad. In the heads of the Cyclorrhapha three secondarily developed, chitinized thickenings (th) arise from the ental surface of the parocciput; two of these project dorso-laterad from the lateral portions of the parocciput, and the third is on the meson. These thickenings are also present in some of the Brachycera, such as Dolichopus (Fig. 112). Their greatest development is found in Eristalis (Fig. 113), where two dorso-lateral thickenings (th) extend to the caudal margins of the compound eyes and a third thickening, on the meson, bifurcates a short distance dorsad of the occipital foramen, the two arms connecting with the dorso-mesal angles of the compound eyes. In the genera figured, the dorso-lateral thickenings are, on the whole, better developed than the thickening on the meson. In Thelaira (Fig. 128) and Musca (Fig. 133) the dorso-lateral thickenings project dorsad to the margin of the head. The area included between them is called by several writers the epicephalon, or the occiput; and tho it is entirely different in origin from similarly situated areas in Tabanus (Fig. 74) and other genera, the same name is applied in the different cases. These names and others used by systematists have no morphological significance for they can not be homologized with the primary sclerites of a generalized insect.

The postgenae (po) of the hypothetical dipterous head have been carefully compared with those of the heads of such generalized insects as the Orthoptera. The mesal membranous area between the postgenae is homologous with the membrane of the neck and with the membrane surrounding the proximal ends of the maxillae and the labium. There are no sutures or sclerites along the mesal portions of the postgenae in such generalized insects as the Orthoptera; consequently the parapostgenae (ppo) described above can not be homologous with any primary sclerite. In Diptera the parapostgenae are undoubtedly special modifications of the postgenae.

The postgenae and the parapostgenae of a majority of the Nematocera resemble those of the hypothetical head. In Chironomus (Fig. 88) and Trichocera (Fig. 78) the parapostgenal thickenings are wanting. The invaginations for the posterior arms of the tentorium in

Simulium (Fig. 77) are adjacent to the occipital foramen, consequently the parapostgenae are confined to the lateral margins of the occipital foramen. In Tabanus also the invaginations are adjacent to the occipital foramen, and the postgenae are connected ventrad of the occipital foramen in the male and by a narrow strip in the female.

The area ventrad of the occipital foramen is a continuous chitinized piece in all of the Cyclorrhapha and the Orthorrhapha. There is only one probable explanation of the origin of this area. It has been derived from the fusion of the mesal margins of the postgenae. The evidence for this interpretation is found in a number of the Nematocera. The mesal margins of the postgenae in Trichocera (Fig. 78) and Sciara (Fig. 81) are curved mesad and in some cases actually join, as in the female of Bibiocephala (Fig. 83). The peculiar elongated heads of Limnobia (Fig. 93), Tipula (Fig. 95), and Psorophora (Fig. 96) show a distinct depressed line on the meson along which the postgenae have joined. In a number of the genera of the Orthorrhapha and the Cyclorrhapha the ventral margin of the caudal aspect is decidedly concave. This condition may be due to a former stage in the development of the fused postgenae. In all cases where the area ventrad of the occipital foramen is chitinized, the invaginations of the posterior arms of the tentorium are somewhat adjacent to the occipital foramen and the attachments of the maxillae are removed to or beyond the ventral margin of the head. Sciara (Fig. 81) is a good example of an early stage in the development of the above relationship. The variations in the shape and extent of the postgenae and the parapostgenae are well illustrated by the figures.

Tentorium.—There is present within the head of generalized insects a definite arrangement of chitinized rods and plate-like structures which go to support the internal organs and furnish places for the attachment of muscles. These rods or plates arise from three pairs of openings on the head known as the invaginations of the anterior arms, dorsal arms, and posterior arms of the tentorium. The invaginations of the anterior arms are usually associated with the lateral margins of the clypeus, with one of the points of articulation of the mandibles, and frequently with the ventral ends of the arms of the epicranial suture. The invaginations of the dorsal arms are associated with the points of attachment of the antennae and near the dorsal portions of the arms of the epicranial suture. The invaginations of the posterior arms are associated with the occipital foramen and the points of attachment of the maxillae. The three pairs of arms unite within the head; the small dorsal arms unite with the larger anterior arms, and these, in turn, join with the posterior arms, which are confined to the caudal portion of the head-capsule. The free ends of the posterior arms are fused and form the body of the tentorium.

The tentorium undergoes a considerable amount of variation in the different orders, but so far as observed the above associations between the invaginations and the fixed and movable parts of the head are always retained by the more generalized members of each order. This is also true for a generalized hpothetical dipterous head. The tentorium (t) of such a head (Fig. 140 and 141) is considerably modified when compared with the tentorium of a generalized insect. Two pairs of invaginations are present on the cephalic aspect of the head (Fig. 1). The dorsal, indistinct pair (i. d), just ventrad of the antennae, are homologous with the invaginations of the dorsal arms of the tentorium, while the prominent pair (i. a) of invaginations ventrad of these and located in the arms of the epicranial suture (a. e. s) and adjacent to the lateral ends of the fronto-clypeal suture are the invaginations of the anterior arms of the tentorium. One pair of invaginations (i. p) is present on the caudal aspect of the head-capsule (Fig. 73) somewhat ventrad of the ventro-lateral margins of the occipital foramen. These are the invaginations of the posterior arms of the tentorium. Each lateral half of the tentorium is Y-shaped (Fig. 141), the stem of the Y arising from the invaginations on the caudal aspect, its caudal portion being a part of the posterior arms (p. a) of the tentorium. The large ventral arm of the Y and the cephalic portion of its stem, constitute the anterior arm (a. a), and the small dorsal arm of the Y is the dorsal arm (d. a) of the tentorium. These two arms connect with their respective invaginations on the cephalic aspect. The body of the tentorium (b. t) is apparently represented by a small, rudimentary, mesal projection arising from the posterior arms near the caudal portion of the stem of the Y.

The association between the movable appendages and the invaginations of the tentorium is discussed under the respective appendages. From this point, the tentorial structures as they occur in the various genera are compared with the hypothetical type and the line of specialization noted. The forms without a ptilinum are considered first. The parts of the free tentorium, not completely fused with the head-capsule, are indicated in the figures by dotted lines.

The tentorium of Tabanus (Fig. 142 and 143) is generalized and closely resembles the hypothetical type; consequently it furnishes a good starting point for a discussion. Two pairs of invaginations are present on the cephalic aspect (Fig. 20); of these the invaginations for the anterior arms (i. a) are the more prominent. The dorsal arms (i. d) arise from the head-capsule just ventro-laterad of the antennae and connect with the arms of the epicranial suture (a. e. s). The invaginations of the anterior arms are situated near the ventral ends of the arms of the epicranial suture. The invaginations on each lateral half of the head are joined together by the arms of the epicranial suture and resemble the hypothetical type. Two pairs of invaginations are also present on the cephalic aspect of Simulium (Fig. 2 and 3), but in this genus they are not as prominent as in Tabanus. They are situated on the vertex (v), adjacent to the compound eyes. In the female the arms of the epicranial suture are well defined and the invaginations are closely adjacent to them, while in the male the sutures are wanting. Tabanus and Simulium are the only forms figured which show two distinct pairs of invaginations on the cephalic aspect. All other genera have only one pair and these are of two types. They are either long and slit-like or they resemble small pits or darkened spots on the ectal surface. The long slit-like invaginations found in Leptis (Fig. 35), Psilocephala (Fig. 36), Platypeza (Fig. 32), Scenopinus (Fig. 41), Exoprosopa (Fig. 29), Stratiomyia (Fig. 27), Mydas (Fig. 30), Eristalis (Fig. 25), and other genera have a special significance which will be more fully discussed later. The small, pit-like invaginations are present in the Nematocera and in Pipunculus (Fig. 38) and Empis (Fig. 40). These are situated on the chitinized area of the vertex; or on the fronto-clypeus, adjacent to the arms of the epicranial suture and usually close to the compound eyes. Their position and structure indicate that they are the invaginations of the anterior arms of the tentorium. In a few of the genera of the Orthorrhapha and in some others, as Lonchoptera (Fig. 37), Tipula (Fig. 18), and Aphiochaeta (Fig. 31), no invaginations are present on the cephalic aspect of the head.

One pair of invaginations, that for the posterior arms (i. p) of the tentorium, is present on the caudal aspect of the heads of all genera examined except Oncodes (Fig. 105), Olfersia (Fig. 139), Tipula (Fig. 95), and perhaps a few species of other genera in which it is difficult to be sure of their presence. These invaginations in Bibiocephala (Fig. 83), Trichocera (Fig. 76), Dixa (Fig. 79), Rhyphus (Fig. 80), Sciara (Fig. 81), Psychoda (Fig. 82), Rhabdophaga (Fig. 86), Chironomus (Fig. 88), Bittacomorpha (Fig. 85), Mycetophila (Fig. 87), and Mycetobia (Fig. 90) are decidedly ventrad of the occipital foramen and adjacent to the proximal ends of the maxillae. They are connected with the lateral margins of the occipital foramen by means of the parapostgenal thickenings except in Chironomus and Trichocera. The abovenamed forms closely resemble the hypothetical type. In a few genera of the Nematocera, such as Psorophora (Fig. 96) and Simulium (Fig. 77), the invaginations are adjacent to the occipital foramen. This position is characteristic of these invaginations in the Brachycera, and the figures show the details of the variations in the position of the invaginations on the posterior arms of the tentorium.

Two lines of specialization appear in the tentorium of the Diptera, one in the reduction of the dorsal arms and the other in the union of the dorsal arms with the anterior arms. The two types of invaginations described for the cephalic aspect of the head bear directly upon this problem. The most important evidence in proof of these two types of development is found in the structure of the arms.

In Sciara (Fig. 150), Bibio (Fig. 153 and 154), Psorophora (Fig. 159), Trichocera (Fig. 158), Bibiocephala (Fig. 155), Dixa (Fig. 163), and others, two long narrow rods extend on each side between the invaginations on the caudal aspect and the invaginations on the cephalic aspect. These rods are composed of the posterior arms (p. a) and the anterior arms (a. a) of the tentorium. The dorsal arms are completely reduced in these forms. Other genera show completely developed dorsal arms or rudiments of the same. The dorsal arms (d. a) are distinct and free in Pipunculus (Fig. 151). They arise from the anterior arms and project cephalad to the cephalic aspect of the head, where they connect with small but distinct ental projections adjacent to the antennae. The cephalic ends of the dorsal arms are very delicate and easily broken in dissecting. There are no invaginations on the ectal surface. In Chironomus (Fig. 152) the tentorial arms are swollen near the middle of their length, and the distinct humps on the dorsal side are interpreted as rudiments of the dorsal arms. Promachus (Fig. 147) has two long, free, finger-like projections, arising from the ocular sclerite near the antennae, which project toward the tentorium proper. These projections are apparently dorsal arms of the tentorium, or derivatives of the same that have retained their connection with the ocular sclerite near the mesal margin of the compound eye but have lost their connection with the tentorium proper. A similar relationship exists between the dorsal arms and the ocular sclerite in Tabanus (Fig. 22). If the above structures in Promachus are dorsal arms, then the anterior arms are large (Fig. 148) and the slit-like invaginations on the cephalic aspect are only the invaginations of the anterior arms of the tentorium.

The tentoria of the Nematocera above described are in the ventral half of the head-cavity and their situation is dependent upon the position of the invaginations. Usually the invaginations of the anterior arms are ventrad of the invaginations of the posterior arms; but Bibiocephala (Fig. 155) is an exception to this rule if the tentorium in this genus is composed of only the anterior and posterior arms—and there is no evidence to the contrary. In some genera, as in Lonchoptera (Fig. 177), Rhabdophaga (Fig. 170), and Empis (Fig. 164), the tentoria are not free rods extending thru the head cavity, but are completely united with the ventral margin of the head, or nearly so. The tentorium of Aphiochaeta (Fig. 174) is reduced to two small ental projections adjacent to the occipital foramen, while in Tipula (Fig. 178) the tentorium is apparently wanting.

In a majority of the Brachycera the tentorial arms are specialized by fusion, and Tabanus (Fig. 143) illustrates an early stage in this development. The principal difference between the tentorium of Tabanus and the hypothetical type is the presence of a thin chitinized plate in the V-shaped opening between the anterior and dorsal arms. Simulium (Fig. 144), of the Nematocera, has a similar plate, and these two genera clearly demonstrate the first stage in the fusion of these two arms. The cephalic end of the tentorium in Mydas (Fig. 146), Leptis (Fig. 145), Scenopinus (Fig. 149), and Exoprosopa (Fig. 162) is a broad uniformly chitinized triangular area. This condition is accounted for on the basis of the union of the anterior and dorsal arms. The invaginations on the cephalic aspect of these forms agree in all respects with this interpretation. In Tabanus (Fig. 20) the invaginations on each side are joined together by the epicranial suture, while in the above forms the invaginations are slit-like and occupy the greater part of the arms of the epicranial suture. The slit-like invaginations are easily explained if the anterior and dorsal arms are considered as united.

The posterior arms of the tentoria of the Nematocera and the Brachycera vary in shape, size, and location. The anterior and posterior arms are united within the head and no sharp line can be drawn between them. The body of the tentorium (b. t) is represented by small projections on the mesal surface of the posterior arms of most genera.

Many interesting features occur in the modifications of the tentoria of this group. In Dolichopus (Fig. 43 and 168) it appears to be fused with the dorsal margin of the slit-like openings on each side between the mesal margin of the compound eye and the fronto-clypeus. The tentorium of Mydas (Fig. 146) is large and tubular, and it is possible to push a good-sized needle thru the opening on the cephalic aspect to the opening of the posterior arms on the caudal aspect.

The tentoria of the genera possessing a ptilinum differ principally from the foregoing in the degree of fusion with the head-capsule. In most genera of this group the tentorium is completely united with the head, but in a number of the Acalyptratae the tentorial arms arise as free rods from the invaginations on the caudal aspect and project to the latero-ventral margins of the head-capsule, with which they unite and continue cephalad as thickenings adjacent to the ventral margin of the head, as in Sapromyza (Fig. 171), Loxocera (Fig. 169), Euaresta (Fig. 175), Calobata (Fig. 183), Chrysomyza (Fig. 181), Drosophila (Fig. 172), Chyromya (Fig. 179), Heteroneura (Fig. 176), and Tetanocera (Fig. 180). In those forms where the tentorium is completely fused with the head, as in Sepsis (Fig. 184), Chloropisca (Fig. 189), Coelopa (Fig. 182), and Borborus (Fig. 188), it is a continuous thickening from the latero-ventral angle of the occipital foramen to the cephalo-ventral aspect of the head-capsule. The tentorium between the invaginations for the posterior arms and the ventro-lateral margins of the head-capsule is apparently wanting in Musca (Fig. 194), Thelaira (Fig. 196), Archytas (Fig. 197), and some other genera; in one or two cases it is possible to trace a faint mark which would indicate the line of connection. The tentoria of some of the genera of the Acalyptratae and the Calyptratae show an unusual development of the tentorial thickenings (t. th) in that they extend about the entire caudal part of the ventral margin of the head. In some cases these tentorial thickenings reach the occipital foramen, as in Calobata (Fig. 114), Scatophaga (Fig. 135), Heteroneura (Fig. 126), Lispa (Fig. 116), and Myiospila (Fig. 120), while in Musca (Fig. 133), Coelopa (Fig. 121), Hydrotaea (Fig. 127), and other genera, there is no such connection.

The invaginations of the posterior arms of the tentorium of the Acalyptratae and the Calyptratae are situated laterad or latero-ventrad of, and adjacent to, the occipital foramen. In many of the species figured the invaginations are merely long, heavily chitinized furrows extending latero-ventrad from the occipital foramen, and very often it is difficult to locate them definitely.

Two mesal projections arise from the proximal portions of the posterior arms in a majority of the Cyclorrhapha. In some species these structures are well developed, and their mesal ends apparently join on the meson, cephalad of the occipital foramen. These structures are similar to those described for the Brachycera and are rudiments of the body of the tentorium.

No invaginations of the tentorium occur on the cephalic aspect in any of the forms which possess a ptilinum. On account of the decided specialization of this aspect, it is very difficult to know just what has happened. The tentorium is represented by thickenings which extend from the ventral to the cephalic aspect of the head. The extent of these thickenings varies; in some genera they continue to the antennal fossae, while in others they are practically wanting.

MOVABLE PARTS OF THE HEAD

In arrangement and structure the movable parts of the head of the generalized Diptera are homologous with the movable appendages of other generalized insects. In the Cyclorrhapha the parts retain their relative position, but structurally they undergo striking modifications and in some cases almost complete reduction.

To make clear the use of a number of terms found in the following discussions, the mouth-parts as a whole will be considered at this point. The appendages of the mouth of the generalized Diptera are free, independent structures, with their proximal ends adjacent to the head-capsule. The cardines and stipites of the maxillae are exceptions to the above statement, in that they are embedded in the mesal membranous area of the caudal aspect of the head. The mouth-parts, the labrum-epipharynx, and the hypopharynx constitute in the Calyptratae a single complex mouth-appendage designated as the proboscis. The chitinized parts of the proboscis are far removed from the head-capsule, but in this projection of the parts, the proximal ends of the chitinized appendages are joined together and have the same relationship with each other as in generalized insects.

The term proboscis is most applicable among the Cyclorrhapha to those whose mouth-parts resemble those of Musca. The proboscis is naturally divided into three areas by the two bends which it makes as it is withdrawn into the oral cavity. The parts of the proboscis have been given varied and confusing names. Hewitt divides it into two general areas—the rostrum and the proboscis proper. He says: ''The proboscis consists of two parts, a proximal membranous conical portion, the rostrum, and a distal half, the proboscis proper, which bears the oral lobes. The term haustellum is also used for this distal half (minus the oral lobes) and as a name it is probably more convenient, as the term proboscis is used for the whole structure,—rostrum, haustellum and oral lobes''.

The terms rostrum and haustellum have been used in various ways by numerous workers in different orders; consequently the parts which they designate are by no means homologous. A more comprehensive set of terms based upon the word proboscis has been used by a few workers, who divide the proboscis into basiproboscis, mediproboscis, and distiproboscis. These terms have here been adopted. The basiproboscis (bpr) is equivalent to the rostrum, and may be defined as the membranous, cone-shaped area between the ventral margin of the head-capsule and the proximal end of the theca. The tormae, labrum-epipharynx, hypopharynx, and maxillae are parts of the basiproboscis. The mediproboscis (mpr) is the median section of the proboscis and includes the theca and the chitinized cephalic groove of the labium. It is equivalent to the haustellum of most authors. The distiproboscis (dpr), the enlarged dilated lobes at the distal end of the proboscis, is composed of the paraglossae, with their pseudotracheal areas, and the glossae. The distiproboscis is equivalent to the oral lobes, or labellae. The movable appendages of the head are discussed in the following order: antennae, mandibles, maxillae, and labium.

Antennae.—The antenna of a generalized hypothetical dipterous head (Fig. 199h) is many-segmented and of a filiform type. All the segments are similar excepting the two large proximal ones known as the scape (sc) and the pedicel (pd). The scape articulates with the chitinized antennal sclerite (a. s) which bounds the periphery of the antennal fossa (a. f) that is situated on the vertex dorsad of the arms of the epicranial suture. The antennae of the hypothetical type resemble the antennae of many generalized insects.

The antennae of a majority of the Nematocera resemble the hypothetical type, and on the whole resemble each other. The variations in shape and size can be seen in the figures. Secondary sexual variation occurs in a few of the Nematocera, in which the antennae of the male, illustrated by Chironomus (Fig. 207) and Psorophora (Fig. 211), bear long flexible setae while those of the female are almost bare.

The antennae of the Brachycera show a wide range of development, but in a majority of the genera figured the main line of specialization is toward the type found in Lonchoptera (Fig. 223) and Dolichopus (Fig. 226). One of the striking exceptions to this general line of development occurs in the geniculate type found in Stratiomyia (Fig. 213). The antennae of the Brachycera have, as a rule, fewer segments than the Nematocera. The scape and pedicel undergo only a slight change, in this group, but the flagellum (fl) is greatly modified. The proximal segment of the flagellum, or the third segment of the antenna, is enlarged, while the remaining segments are so reduced in size as to resemble the lash of a whip. The lash-like portion of the antenna is called the arista (ar). The following genera suggest the various stages thru which the antennae have passed in attaining the muscid type of development. In Tabanus (Fig. 214), Empis (Fig. 215), Exoprosopa (Fig. 216), Promachus (Fig. 217), and Leptis (Fig. 218) the flagellum is stylate, and the third segment is large and conical, with one or more segments at its distal end. The antennae of Platypeza (Fig. 222), Lonchoptera (Fig. 223), Aphiochaeta (Fig. 224), Oecothea (Fig. 227), and Dolichopus (Fig. 226) show an advanced stage of development in which the third segment is large and round and the remaining segments are lash-like and situated toward one side of the third segment. All but a few of the antennae of the Cyclorrhapha have apparently developed from a type similar to the last-mentioned genera. The principal differences between the antennae of this group are in the length and breadth of the third segment and in the modification of the arista. The antennae of Olfersia (Fig. 249) are of a reduced muscid type, and are inserted in deep cavities on the cephalic aspect of the head; the scape and pedicel are greatly reduced, and the arista is merely a small projection on the lateral aspect of the large segment.

Antennal sclerites (a. s) are present only in Chironomus (Fig. 12 and 206) and Psorophora (Fig. 10 and 26). In these genera it is a distinct chitinized ring about the proximal end of the scape. The extent and place of the membrane with which the antennae are connected vary considerably. In Trichocera (Fig. 16), Chironomus (Fig. 12), Psorophora (Fig. 26), Mycetobia (Fig. 7), and some other genera it is very extensive.

A general survey of the antennae of the Diptera shows that in the Nematocera they are generalized and on the whole resemble each other. The specialized antennae of the Cyclorrhapha in all but a very few genera are of a muscid type, and also quite similar in form. The antennae of the Brachycera present a few specialized types, but the majority of them show intermediate stages between the forms found in the Nematocera and those of the Cyclorrhapha.

Mandibles.—Only a few of the generalized Diptera possess mandibles. They are present in the females of Simulium (Fig. 2 and 250), Tabanus (Fig. 255 and 317), Psorophora (Fig. 159 and 251), Culicoides (Fig. 253), Dixa (Fig. 254), and Bibiocephala (Fig. 155 and 256), but wanting in the males of all the species examined except Simulium (Fig. 3 and 252). The males of *Simulium johannseni* and *S. jenningsi* have distinct mandibles. No other males of Simulium were examined. So far as known this is the first record of a male dipteron possessing true mandibles.

The hypothetical mandibles (Fig. 256h) of a dipteron are long, thin, sword-shaped structures fitted for piercing. They thus resemble the mandibles (md) of Tabanus (Fig. 255) and Culicoides (Fig. 253). They are situated between the clypeus, labrum-epipharynx, and maxillae, and are closely associated with the invaginations of the anterior arms of the tentorium. Structurally the hypothetical mandibles do not resemble the biting mandibles of the Orthoptera, but their situation and their association with the invaginations of the anterior arms of the tentorium are the same, which is far more important in determining their homology than any particular form they may assume.

The mandibles vary in their structure. In Psorophora (Fig. 251) they are long and needle-like, while in Tabanus, Culicoides, and the male of Simulium (Fig. 252) they are sword-shaped, and in Dixa (Fig. 254) spindle-like. The mandibles in the females of all species of Simulium (Fig. 250) examined are a trifle longer than those in the males (Fig. 252) and much broader at their distal ends. The greatest specialization in structure and point of attachment with the head occurs in the long, thin, saw-like mandibles of Bibiocephala (Fig. 256) and Blepharocera. In these forms they are longer than the labium, blunt at the end, and toothed along the mesal margin, fitting against a similar edge on the lateral margin of the hypopharynx.

All mandibles (md) of the Diptera are connected with the head-capsule cephalad of the maxillae (mx) and caudad of the labrum-epipharynx (l. ep) and the fronto-clypeus (fr. c). In this respect they resemble the hypothetical type. In Psorophora, Dixa, Simulium, and Tabanus they are associated with the invaginations of the anterior arms of the tentorium. The proximal ends of the mandibles of Psorophora (Fig. 159) are bent cephalad, and articulate with the head-capsule at the distal ends of the crescent-shaped tentorial thickenings (t. th) which arise from the margins of the invaginations of the anterior arms of the tentorium. In Dixa (Fig. 254) the mandibles connect with the head-capsule at the ventro-caudal angles of the clypeus. An indistinct thickening extends dorsad from the point of articulation of each of the mandibles toward the invaginations of the anterior arms of the tentorium. The mandibles of Simulium (Fig. 250 and 252) and Tabanus (Fig. 317) connect with the head-capsule directly ventrad of the invaginations of the anterior arms of the tentorium, but no direct connection occurs between them. In the female of Simulium the mandibles articulate with a hook-shaped projection of the vertex. The mandibles of Tabanus (Fig. 255) are bifurcate at their proximal end and the lateral bifurcation articulates with the head. The location of the mandibles of Bibiocephala (Fig. 155) and Blepharocera is generalized with respect to their position between the maxillae and the fronto-clypeus, but their point of attachment with the head-capsule is decidedly specialized. They unite with chitinized pillars (Fig. 83) on the caudal aspect ventro-laterad of the invaginations of the posterior arms of the tentorium. The proximal portion of each mandible is a long chitinized strip embedded in the membrane. These strips extend cephalad from their caudal connection to the cephalic margin of the membrane about the mouth-parts. At this point, where distinct tendons are attached, they turn abruptly ventrad and become free appendages. All connection between the mandibles and the invaginations of the anterior arms of the tentorium is lost. The relationship between the tentorium and the mandibles has not been observed in Culicoides for the lack of material. No other families of the Diptera outside of those to which the above-named genera belong, so far as observed, possess true mandibles or rudiments of the same. When mandibles are present, they are always of considerable size and probably functional.

A number of investigators have described mandibles for many species not included in the above families. Langhoffer (1901) describes mandibles for the Dolichopodidae which are shown in this paper to be modifications of the epipharynx (Fig. 524 and 528). The apodemes of the muscids (Fig. 304, 308, and others) have been called mandibular tendons by MacCloskie and others. This is incorrect as shown by the figures and in the discussion of the maxillae. A number of workers (e. g., Wesché, 1909) believe that the mandibles have united with the labium and exist as chitinized strips on the cephalic aspect of the labium or as thickenings on the meson of the theca. Neither of these interpretations can be accepted when one takes into consideration the relative position of these so-called mandibles and the manner of development of the proboscis of the Calyptratae. The chitinized thickenings on the cephalic aspect of the labium are located caudad of the maxillae and the hypopharynx. This does not agree with the position of the mandibles of other insects. Furthermore, these thickenings are present in Tabanus where true mandibles occur. The chitinized thickenings on the meson of the theca in some of the Diptera can not be considered as rudiments of mandibles for many reasons. The most conclusive objection to this interpretation lies in the fact that these thickenings are very prominent in Simulium which has distinct mandibles in both sexes.

When interpreting mouth-appendages, it is always necessary to take into consideration the generalized relationship between the mouth-parts and their association with the invaginations of the tentorium. It is also very desirable to observe a large series of forms before attempting to homologize the parts. The above interpretations were apparently not made from either of these vantage-points.

Maxillae.—All Diptera having functional mouth-parts have maxillae. They are, however, greatly reduced and modified in some genera, and at first glance bear little or no relation to the structure or location of the maxillae of generalized Diptera or other insects. Numerous intermediate stages of maxillary development are present in the various species; consequently it is possible, and in fact comparatively easy, to trace thruout the order the main line of specialization and several side lines.

The hypothetical maxillae of the Diptera (Fig. 257) resemble the maxillae of a generalized insect in their homologous sclerites, their position between the mandibles and the labium, and their close association with the invaginations of the posterior arms of the tentorium. Structurally they are composed of small triangular cardines (ca), long stipites (st), five-segmented palpi (mx. pl), needle-like galeae (g), and short laciniae (la). The cardines and stipites differ from those of generalized insects in that they are embedded in the mesal membranous area ventrad of the occipital foramen. The palpi, galeae, and laciniae are free appendages. The proximal ends of the cardines are adjacent to the invaginations of the posterior arms of the tentorium. The structure and position of the various parts of the hypothetical type have been traced thruout the order. The species in which the ptilinum is wanting are considered first.

The cardines (ca) are small distinct triangular sclerites in Trichocera (Fig. 260), Rhyphus (Fig. 261), Dixa (Fig. 262), and the female of Tabanus (Fig. 259). In these genera they are adjacent to the invaginations of the posterior arms of the tentorium. The cardines of Simulium (Fig. 258), in both males and females, differ from those of the above genera in that they are large and occupy nearly all of the membranous area between the postgenae dorsad of the stipites. Their margins are also somewhat indistinct. No other forms figured have distinct sclerites that are homologous with the cardines of the hypothetical type. The maxillae of Rhabdophaga (Fig. 268), Bibiocephala (Fig. 269), and Chironomus (Fig. 270) connect with the invaginations of the posterior arms by means of narrow chitinized processes which arise from the stipites proper. Undoubtedly these pieces are reduced cardines which have lost the suture that separates them from the stipites. The presence of this suture is suggested by the suture-like depression in the male of Bibiocephala (Fig. 76). Excepting Promachus (Fig. 276) and the above forms, the cardo is wanting in all the maxillae figured. The maxillae of Psychoda (Fig. 263) and Sciara (Fig. 267) closely resemble some of the above maxillae, but the cardines as chitinized pieces are apparently wanting. There is a distinct membranous area between the proximal ends of the stipites and the invaginations of the posterior arms of the tentorium. From forms such as these it is concluded that the cardines have been lost as chitinized areas. No other interpretation seems possible with the evidence at hand.

The stipites (st) are of various shapes and sizes as can be seen in the figures. In Rhabdophaga (Fig. 268), Bibiocephala (Fig. 269), Chironomus (Fig. 270), and possibly Mycetobia (Fig. 90), they have united to form a chitinized strip or plate in the membranous area dorsad of the labium. This piece should not be confused with the submentum of the labium. In all species in which the postgenae have not united ventrad of the occipital foramen, the proximal ends of the stipites are near the invaginations of the posterior arms of the tentorium. In all species where the postgenae form a continuous plate, the stipites are reduced in size and situated at or beyond the ventral margin of the head, as in Mydas (Fig. 319) and Eristalis (Fig. 328). In other words, the usual association between the maxillae and the invaginations of the posterior arms has been lost. Psilocephala (Fig. 281) and Psorophora (Fig. 96) are exceptions to the last statement. In Psilocephala chitinized thickenings (ch. th) are present on the ental surface of the postgenae ventrad of the occipital foramen, and these are undoubtedly rudiments of the stipites. The stipites of Psorophora (Fig. 266 and 96) are long, free rod-like structures located entad of the postgenae. They extend between the occipital foramen and the ventral margin of the head. The stipites of Geranomyia (Fig. 382) and Limnobia (Fig. 386) are also entad of the postgenae. In these genera their proximal ends are united and they have no connection with the head-capsule. The stipites of Tipula (Fig. 277) resemble those of Geranomyia and Limnobia, but there is greater reduction in size, and they are completely united along their mesal margins, thus forming a single median piece.

The maxillae of Promachus (Fig. 84) differ from those of all other genera in that the stipites and the cardines are united on the meson and continuous with the postgenae near the occipital foramen. Narrow membranous areas separate the maxillae from the postgenae near the ventral margin of the head. This unique modification of the maxillae agrees with the striking modifications in the other mouth-parts.

The figures show the variations in other genera belonging to this group. In general it can be said that the stipites have been modified by reduction and by removal to the ventral margin of the head and in some cases are even located on the basiproboscis.

The maxillary palpi (mx. pl) of the Nematocera figured have from two segments—Geranomyia (Fig. 382) and the female of Psorophora (Fig. 266)—to five segments. The usual number is four or five. In the Brachycera only one articulating segment is present. This segment in Tabanus (Fig. 259) connects with an elongated portion of the stipes which is called the palpifer by some. In this study the palpifer is considered as wanting, since no palpus of the Diptera possesses over five segments and furthermore no piece is present at the base of any generalized palpus which can be homologized with the palpifer of generalized insects. The greatest reduction in the palpus of the Nematocera occurs in Geranomyia (Fig. 382), while in the Brachycera the palpus of Mydas (Fig. 271) is a mere lobe.

A small finger-like structure arises from the ventro-mesal margin of each stipes and projects mesad to the caudal aspect of the hypopharynx in Tabanus (Fig. 259) and Simulium (Fig. 258). These pieces are apparently homologous with the laciniae (la) of generalized insects. The distal ends of these projections articulate against the caudal aspect of the hypopharynx (Fig. 496 and 497), and in this respect they differ from the laciniae of generalized insects. These pieces in Tabanus have been described as laciniae by Patton and Cragg (1913).

A distinct lobe is present mesad of the palpus in the majority of the Diptera that do not have a ptilinum. This structure is unquestionably the galea (g), for in specialized insects which possess a distinct galea the lacinia is generally reduced in size and in some cases wanting. This tendency of development prevails in the Diptera. If the above pieces in Tabanus and Simulium which are described as laciniae are truly such, there can be no question regarding this interpretation of the lobe adjacent to the palpus. The galeae vary considerably in size and shape. They are long and needle-like in Tabanus (Fig. 259), in the female of Psorophora (Fig. 266), and in Empis (Fig. 274), Exoprosopa (Fig. 285), and Eulonchus (Fig. 284a); while in Trichocera (Fig. 260), Dixa (Fig. 262), Sciara (Fig. 267), Bittacomorpha, Chironomus (Fig. 270), Lonchoptera (Fig. 280), Scenopinus (Fig. 282), and the male of Psorophora (Fig. 266) they are greatly reduced. In Bibio (Fig. 264) and Geranomyia (Fig. 382) they are mere rudiments. They are wanting in Rhabdophaga (Fig. 268), Tipula (Fig. 277), Helobia (Fig. 385), Aphiochaeta (Fig. 278), Pipunculus (Fig. 279), Platypeza (Fig. 272), and Dolichopus (Fig. 284).

The development of the maxillae of the genera possessing a ptilinum will now be considered. No cardines or laciniae are present in this group. The maxillary palpi are one-segmented and are present in all forms except Conops (Fig. 305). The palpi interpreted here as maxillary palpi have been called labial palpi by some (e. g., Wesché, 1909). The stipites and galeae are present in all the species studied, and they undergo decided morphological changes. All connection or association between the maxillae and the invaginations of the posterior arms of the tentorium has been lost. This loss is even more pronounced than in the Brachycera, since in all but a few species figured the maxillae are far removed from the head and situated near the distal end of the well-developed basiproboscis. This migration of the maxillae in the Cyclorrhapha has not altered their generalized position between the labrum-epipharynx and the labium.

The stipites of genera having a ptilinum show all stages of ingrowth from a turned-in free edge or end (st-e), to forms in which it is entirely entad of the membrane of the basiproboscis, as in Musca. Eristalis (Fig. 286), Eulonchus (Fig. 284a), and Exoprosopa (Fig. 285) are the only forms without a ptilinum which show an ental growth of the stipites. These genera make a good starting point for explaining the characteristic development found in the Acalyptratae and the Calyptratae. The following scheme of lines and dots has been adopted on the drawings in order to show the degree of ingrowth of the stipes. A continuous solid line on the stipes indicates a definite ectal boundary which connects with the membrane of the basiproboscis. A broken line indicates an ental edge or end which is free of the membrane between it and the observer. The membrane is represented by stippling. For convenience of description and homology the following division of the stipes has been made: st represents the ectal portion of the stipes and st-e the ental portion; and st is further divided into st-1 and st-2 as seen in Coelopa (Fig. 288).

In Exoprosopa (Fig. 285) and Eulonchus (Fig. 284a) the proximal end of the stipes is free and entad of the membrane, while the cephalic edge and the dorsal end are entad in Eristalis (Fig. 286). From a form similar to Eristalis it is possible to develop a stipes which would resemble that of Sepsis (Fig. 287), Coelopa (Fig. 288), and Calobata (Fig. 296). In Sepsis the palpus is greatly reduced, but it connects with an ectal portion of the stipes (st) which in turn gives rise to the free ental portion (st-e). The free ental part extends ventrad and is continuous with the galea, which emerges from the membrane near the base of the labrum as a free appendage. The stipes of Coelopa (Fig. 288), Sapromyza (Fig. 289), and Sphyracephala (Fig. 293) is similar to that of Sepsis, but in these forms the palpus arises from the cephalic margin of the basiproboscis. The palpus is connected with the stipes proper by means of a long chitinized strip (st-1) which is usually covered with setae. This ectal portion of the stipes (st-1) is present in all but a few genera, such as Chloropisca (Fig. 306), Heteroneura (Fig. 298), Chyromya (Fig. 299), Loxocera (Fig. 300), and Euaresta (Fig. 292). In a number of forms, particularly in the Calyptratae, a small chitinized area is present ventrad of the palpus. This is regarded as a secondary chitinization. The ectal portion of the stipes (st-2) is present in a majority of the Acalyptratae and in one or two of the Calyptratae.

The ental portion of the stipes (st-e) is always present in the members of this group. In Desmometopa (Fig. 303), Chloropisca (Fig.

306), Conops (Fig. 305), and the Calyptratae it has no connection with the ectal portion of the stipes (st-2) or the membrane, and by many writers is commonly called the apodeme. The free so-called apodeme is unquestionably derived from the ental ingrowth of the stipes, as illustrated by the modifications found in the following genera: Coelopa (Fig. 288), Sapromyza (Fig. 289), Tetanocera (Fig. 297), Archytas (Fig. 309), Musca (Fig. 304), and others.

The development of the galea (g) may be traced thruout the Cyclorrhapha in a manner similar to that of the stipes. In Eristalis (Fig. 286) the galea is a long free appendage arising from the ventral end of the stipes near the proximal end of the labrum-epipharynx. Its length and size are greatly reduced in Sepsis (Fig. 287), but its position is identical with that of Eristalis. Thruout the majority of the Acalyptratae the position of the galea resembles that of Sepsis. Its size and form undergo some change, as can be seen in the figures. In the Calyptratae and some of the Acalyptratae the galea articulates with the proximal end of the labrum and is more or less firmly connected with the same. The ectal exposure of the galea is very small in these forms. The large galea of the Acalyptratae has been considered as the maxillary palpus by Wesché (1902). This interpretation is highly improbable.

Labium.—The labium is the most specialized and characteristic appendage of the mouth of Diptera. Its structural modifications are very striking among the specialized genera, such as the Cyclorrhapha. These modifications are largely due to the reduction of the parts and the excessive development of membranous areas, and they agree with similar types of modification in other head- and mouth-parts.

To explain the unique development of the labium of Diptera, it has been necessary to make a critical study of the generalized condition of this appendage as it occurs in the Nematocera and to compare it carefully with the labia of more generalized insects. As is well known, the labium of a generalized insect is the posterior, independent, flap-like mouth-part, made up of a submentum, mentum, and ligula. The ligula is further divided into palpigers, palpi, paraglossae, and glossae. The labium of a generalized dipteron resembles that of a generalized insect in its caudal position and in its independent condition, but it is very different in structure. It is more or less enlarged and not flat and flap-like, and the palpi and palpigers are always wanting, so far as observed. Since the position of the palpi and the palpigers is very useful in orienting the sclerites of the labium of generalized insects, their absence in Diptera makes it exceedingly difficult to homologize correctly and locate the submentum, mentum, and the parts of the ligula. The membranous condition of the labium also adds to this difficulty.

In order to get some light on this problem, a study was made of the labium, particularly the submentum and mentum, of a number of generalized insects of the more common orders. The literature of this subject was examined, but no satisfactory results were obtained from this source. After a careful study of a number of labia, the following general characteristics which bear upon the labium of Diptera, were noted. The submentum is the large proximal segment, while the mentum is usually small and in some cases very thinly chitinized and almost obsolete. The sutures separating the mentum from the submentum and the ligula are only represented by small remnants in Melanoplus. The ligula, so far as observed, comprises the movable parts of the labium, while the mentum and submentum are more or less firmly united with the head-capsule. The proximal part of the ligula is usually well developed and gives rise to the palpigers, palpi, paraglossae, and glossae. The glossae are located between the paraglossae, and in a number of forms a distinct depression or thickening extends proximad between the glossae and the proximal margin of the ligula.

With these observations as a basis for comparison, the labium of such generalized Diptera as Chironomus (Fig. 371), Simulium (Fig. 366), Trichocera (Fig. 365), Dixa (Fig. 375), and others may be interpreted as follows. The mesal membranous area of the caudal aspect of the head, which is bounded by the postgenae (po), the occipital foramen (o. f), and the proximal chitinized piece of the labium (the), is made up of the submentum, mentum (su. me), and the cardines (ca) and stipites (st) of the maxillae (mx). Since this area is largely membranous, it is impossible to determine the boundaries of these sclerites. The areas laterad of the cardines and the stipites apparently belong to the maxillae, while the area mesad of these parts is made up of the submentum and mentum (su. me). The important feature concerning this mesal membranous area is the fact that the maxillae and the labium both play a part in its formation. This undoubtedly indicates that the submentum and mentum, of a more or less fixed nature in generalized insects, have been more extensively fixed in the Diptera, and that the submentum and mentum are included in the membrane developed from the stipites and cardines. Such an interpretation is altogether possible, since the proximal portions of the maxillae are adjacent to the submentum and mentum in generalized insects.

The ligula (lg) of the generalized Diptera agrees with the ligula of generalized insects in that it is the movable part of the labium. Structurally it is composed of a well-developed proximal area which gives rise to two large bulb-like paraglossae (pgl) and to two small membranous glossae (gl) which are located between the paraglossae. The palpigers and labial palpi are wanting, but if in the future some form is discovered which shows these structures, they will undoubtedly be found on the area here described as the ligula. The proximal portion of the ligula has a decided furrow or thickening on its caudal aspect along the meson. This thickening is characteristic of a number of Diptera and resembles the proximal portion of the ligula of a number of generalized insects. This mesal thickening marks the line of fusion of the two parts of the labium during embryonic development.

The above interpretation of the labium is on the whole very satisfactory for the numerous modified types found in the various families of the Diptera, and with this interpretation it is possible to formulate a hypothetical labium. This has been done in this study; but there have been added to this labium the early stages of development of the more important secondary structures which are characteristic of the labia of Diptera. It will therefore be advisable to call such a hypothetical labium a typical labium in order to distinguish it from the true hypothetical type of other parts of this study.

A typical labium of the Diptera (Fig. 1, 73, 140, 362, and 363) is made up of a submentum, mentum, and ligula. The submentum and mentum (su. me) are firmly united with the head and constitute the greater portion of the mesal membranous area of the caudal aspect of the head. The ligula (lg) is the large swollen and movable portion of the labium and consists of the mediproboscis (mpr) and the distiproboscis (dpr). The mediproboscis has a chitinized area on its caudal aspect which is commonly called the theca (the). The distiproboscis is composed of two large membranous bulb-like paraglossae (pgl) and two small membranous glossae (gl) which are located between the proximal parts of the paraglossae. The important and characteristic features of a typical labium are the chitinized pieces on the caudal and lateral aspects of the paraglossae and the trachea-like structures on the mesal aspects. The details of the various parts will be more fully discussed as each part is considered and its modification traced thruout the order.

The submentum and mentum (su. me) are present as a membranous area in a majority of the Nematocera and in the females of Tabanus (Fig. 74). This area undergoes considerable modification, as was seen in the discussion of the maxillae and postgenae, and is illustrated by the figures. Rhyphus (Fig. 80 and 374) is apparently the only genus which has within this area a chitinization which can not be considered as a modification of the maxillae or of the postgenae. This piece is a more or less distinctly chitinized, inverted-flask-shaped area between the maxillae. If this is a primary chitinization, it is probably a remnant of the submentum. A similarly situated area found in Mycetobia has been homologized by some writers with that of Rhyphus. This interpretation is undoubtedly incorrect, since this area in Mycetobia (Fig. 90) gives rise to chitinized projections at its ventro-lateral angles and these in turn connect with the maxillary palpi and the galeae. Furthermore, the relationship which this piece bears to the proximal end of the theca (the) would tend to disprove such an interpretation. This piece in Mycetobia is undoubtedly a specialization of the maxillae similar to the modifications found in Bibiocephala (Fig. 83) and Rhabdophaga (Fig. 86). In all genera where the postgenae have grown together on the meson the submentum and mentum have been eliminated, unless one regards the area between the ventral margin of the head and the theca as derived from these areas. This area, as already described for the Cyclorrhapha, is very extensive and forms the caudal portion of the basiproboscis (bpr).

The proximal portion of the ligula or mediproboscis (mpr) of the typical labium is largely membranous, but it has on its caudal aspect a distinctly chitinized area, the theca (the), which has a distinct furrow on its meson. The shape, size, and degree of chitinization of the theca vary greatly, as can be seen in Bibio (Fig. 364), Trichocera (Fig. 365), Rhyphus (Fig. 374), Promachus (Fig. 376), Tabanus (Fig. 391), Chyromya (Fig. 411), Conops (Fig. 420), Rhamphomyia (Fig. 424), and Musca (Fig. 466). There is a distinct furrow or thickening on the meson of the majority of the Nematocera and the Brachycera, and remnants of these thickenings occur also among the Cyclorrhapha. In some of the Diptera the structural condition of the meson has a marked influence on the shape of the dorsal and ventral margins of the theca. The cephalic aspect of the proximal portion of the ligula of a typical labium is concave and membranous and connects with the proximal part of the lance-like portion of the hypopharynx. In the Nematocera the cephalic aspect resembles the typical labium, and in the Brachycera and in a majority of the Cyclorrhapha it has a distinctly chitinized groove. This is well illustrated by Tabanus (Fig. 392), Eristalis (Fig. 441), and a majority of the Calyptratae. The degree of chitinization varies considerably, and in some forms heavy, chitinized, cord-like pieces extend along the sides of the groove from the glossae to the proximal end of the labium.

The distiproboscis of the typical labium is composed of two large independent, highly membranous, bulb-like paraglossae (pgl), usually called oral lobes or labellae, and two small membranous glossae (gl). Each paraglossa has on its lateral and caudal aspects a Y-shaped chitinized support which has been commonly called the furca. For convenience in description and as an aid in tracing the development of the parts of the furca thruout the order, it has been divided into furca-1, which is the stem of the Y, furca-2, which is the dorsal arm of the Y, and furca-3, which is the ventral arm. The furca articulates with a small sclerite which is located between the proximal end of furca-1 and the distal end of the chitinized furrow on the meson of the theca. This piece has been called the sigma (si). Another small, independent sclerite is located in the membrane just laterad of the sigma and this may be known as kappa (k). Each paraglossa has on its mesal aspect two trachea-like structures which arise from the proximal portion of the glossa. These structures are commonly called pseudotracheae (ps).

A general survey of the characteristics of the paraglossae of the various labia shows that they are usually bulb-like, membranous, and somewhat flexible. In these respects they differ decidedly from the firmly chitinized, flap-like labia of many generalized insects. Their size and shape vary greatly, as can be seen in Bibio (Fig. 364), Leia (Fig. 368), Promachus (Fig. 376), Geranomyia (Fig. 382), Tipula (Fig. 384), Tabanus (Fig. 390), Conops (Fig. 417), Empis (Fig. 421), Siphona (Fig. 458), Musca (Fig. 467), Stomoxys (Fig. 479), and Olfersia (Fig. 488). The use to which the labia are put seems to have some influence on their form. The main line of development thruout the genera figured is toward the type found among the Calyptratae, in which the labia are usually large, decidedly membranous, and joined together on the dorso-caudal areas, as in Hydrotaea (Fig. 475), Sarcophaga (Fig. 477), Sepsis (Fig. 439), Loxocera (Fig. 461), Tetanocera (Fig. 463), and many other genera.

The membranous development of the paraglossae is not always a good indication of the main line of specialization. In a number of scattered genera, Chironomus, Rhyphus, Aphiochaeta, Chloropisca, Platypeza, Leptis, Psilocephala, and Lonchoptera, it is next to impossible to make out the chitinized pieces, such as kappa, sigma, and furca, because of the membranous condition of the entire labium. Outside of the above-named forms, the chitinized pieces of the paraglossae are usually distinct when present. These supports may be secondary in origin or they may be remnants of former chitinized parts of the paraglossae. It is possible to show how the various chitinized pieces of the majority of the labia may have been developed from the typical form.

The sclerite designated as kappa (k) on the typical labium is only present in Tabanus (Fig. 390 and 391), Tipula (Fig. 388), and Bittacomorpha (Fig. 85). No other dipteron gives any evidence whatever of such a sclerite. In the above-mentioned genera the pieces are embedded in the membrane laterad of the ventral ends of the theca. Some one has interpreted these pieces as rudimentary palpigers or palpi. This may or may not be correct. It is possible for palpi to be in such a position; but since no other genera have similar pieces, and since they are so decidedly dissimilar to the labial palpi and palpigers of generalized insects, they are here regarded as secondary sclerites.

The sclerite designated as sigma (si) is present as a chitinized thickening at the ventral end of the theca, as in Eristalis (Fig. 443), or as a distinct piece, as in a majority of the Brachycera and the Cyclorrhapha. In all genera it is situated between the ventral margin of the theca and the furca. Only a few genera of the Nematocera, such as Tipula (Fig. 388) and Psorophora (Fig. 380), have these sclerites. They undergo some modification in size and structure as can be seen in the following genera: Tabanus (Fig. 391), Mydas (Fig. 397), Conops (Fig. 418), Borborus (Fig. 437), Eristalis (Fig. 443), Coelopa (Fig. 448), and Scatophaga (Fig. 470).

The furca of Bibio (Fig. 315) and that of Tabanus (Fig. 317) closely resemble the typical form. In Bibio, furca-1 (f-1) and furca-2 (f-2) are one continuous piece, while furca-3 (f-3) is a distinct arm. In Tabanus, furca-2 and furca-3 are distinctly chitinized areas arising from the distal end of furca-1. Only one chitinized support is present in Sciara (Fig. 314), Rhabdophaga (Fig. 313), Psychoda (Fig. 318), Stratiomyia (Fig. 331), and Trichocera (Fig. 311). In Trichocera this support has a decided dorsal bend near the constriction of the paraglossae. This bend is also present in Psychoda and Stratiomyia, but the constriction is wanting. The distal portion of the furca beyond the bend is homologous with furca-2, and furca-3 is wanting in these forms. Furca-2 is present and furca-3 is wanting in Scenopinus (Fig. 325); furca-3, however, is present in more species than furca-2. Such is the case with Borborus (Fig. 342), Chrysomyza (Fig. 341), Coelopa (Fig. 337), Tetanocera (Fig. 344), Scatophaga (Fig. 357), Musca (Fig. 351), and Thelaira (Fig. 346).

Furca-1 (f-1) varies considerably thruout the order. In generalized forms where the dorso-caudal portions of the paraglossae are not joined together the furcae are always well separated. They are also separated in some forms where the paraglossae are joined, as in Mydas (Fig. 397) and Eristalis (Fig. 443). In Chyromya (Fig. 411), Drosophila (Fig. 454), Tetanocera (Fig. 463), and Sepsis (Fig. 439), an intermediate piece joins the mesal ends of furcae-1 while in Sarcophaga (Fig. 477), Musca (Fig. 466), Coelopa (Fig. 448), Sapromyza (Fig. 409), Chrysomyza (Fig. 457), Heteroneura (Fig. 459), and Oecothea (Fig. 452) furcae-1 are united and form one continuous U-shaped piece. This type of furcae is present among the Calyptratae. The furcae of specialized forms, such as Olfersia (Fig. 488), Conops (Fig. 418), Siphona (Fig. 355), Empis (Fig. 421), and others, are not differentiated, since the greater part of the lateral aspects of the paraglossae is chitinized.

In the typical labium two simple trachea-like structures, commonly known as pseudotracheae (ps), arise from the proximal part of each glossa and extend onto the mesal membranous aspect of each paraglossa. These trachea-like structures are in reality small chitinized troughs which serve as conduits for the liquid food. Pseudotracheae are unique structures and peculiar to Diptera, so far as known. They are present in only a few generalized forms, but from these genera it is possible to develop the pseudotracheal arrangement and structure of the more specialized Diptera. It is consequently assumed that the pseudotracheae have probably arisen only once within the order, and that this happened some time after the group as a whole was set off as a distinct order.

The psedotracheae (ps) of Tipula (Fig. 383) resemble those of the typical labium in that the two main pseudotracheae arise from each glossa and extend over the mesal membranous area of the paraglossa, one of the pseudotracheae extending caudad and the other cephalad. These ducts are secondarily branched and resemble a fern. The pseudotracheae of Mycetophila (Fig. 11) and Leia (Fig. 368) are reduced and only the caudal pseudotracheae extend over the paraglossae. The paraglossae in these genera are united along the meson and form a single large lobe. The cephalic pseudotracheae are indicated by small rudiments in Mycetophila (Fig. 11). The pseudotracheae in these forms resemble the typical labium in that they are simple, unbranched, chitinized troughs. From the typical labium, or from the pseudotracheae as they occur in Tipula, it is possible to derive the arrangement and structure of the pseudotracheae as they are found in Tabanus (Fig. 390) and similar forms, where two long pseudotracheal trunks (m. ps) extend cephalad and caudad from the glossae (gl) and give rise to many branches on their ventral side. These branches extend ventrad over the entire mesal area of the paraglossa (pgl). The arrangement of the pseudotracheae of most Diptera is readily derived from a form similar to Tabanus. The arrangement in Scenopinus (Fig. 400), Psilocephala (Fig. 403), and many of the Calyptratae resembles that in Tabanus. In such genera as Stratiomyia (Fig. 396), Oecothea (Fig. 453), Coelopa (Fig. 449), and Heteroneura (Fig. 460) no main collecting ducts (m. ps) extend beyond the glossae. In many genera, such as Chloropisca (Fig. 431) and Chyromya (Fig. 412), no line of demarkation can be drawn between the proximal ends of the pseudotracheae and the glossae.

U-shaped or open ring-like thickenings are present in the pseudotracheae of the more specialized Diptera. They do not occur in the simple pseudotracheae of Mycetophila or in some of the highly specialized forms. The histological structure of a pseudotrachea has been clearly demonstrated by several workers. According to Dimmock, "The pseudotracheae on the inner surfaces of the labellae of Musca are cylindrical channels, sunk more or less deeply into the surfaces of the labellae according to the amount that that surface is inflated, and they open on the surface in zig-zag slits. These channels are held open by partial rings, more strongly chitinized than the rest of the membrane of the cylinder. As seen from above in Musca, [Fig. 485], the pseudotracheae appear to be supported by partial rings, one end of each of which is forked. . . . . . The pseudotracheae of Eristalis are so nearly like those of Musca [Calliphora] vomitoria that I have not figured those of the former." All my observations of the histological structure of pseudotracheae agree with those made by Dimmock. Tho no attempt was made to work out the detail of the histological structure in the various genera studied, a number of interesting facts were observed. The chitinized, taenidia-like thickenings (ps. th) in Ochthera (Fig. 445 and 483) are large U-shaped structures which are partially embedded in the membrane. The ends of these thickenings project considerably beyond the surface of the membrane and resemble these structures in *Bombylius major* (Fig. 482), as figured by Dimmock. The pseudotracheae of Calobata (Fig. 446) have developed into rows of small chitinized teeth (tee).

The pseudotracheal area of the paraglossae undergoes its greatest specialization in forms in which the paraglossae assume a biting function. This biting type is brought about by the development of distinct chitinized teeth arising between the proximal ends of the pseudotracheae. Rudimentary or well-developed teeth occur in Musca (Fig. 467), Sarcophaga (Fig. 478), Scatophaga (Fig. 472), Lispa (Fig. 481), and Stomoxys (Fig. 480). In Musca the small, chitinized, so-called prestomal teeth (tee) are present between the proximal ends of the pseudotracheae. In Scatophaga and Lispa these teeth are large and distinct. Their greatest development occurs in Stomoxys, and so far as observed pseudotracheae are wanting in this form. An extensive discussion of the development and the structure of the chitinized teeth of the paraglossae has been given by Patton and Cragg (1913).

The glossae (gl) of a typical labium (Fig. 1 and 73) are two small lobes located between the proximal portions of the paraglossae distad of the furrow on the theca and at the distal end of the cephalic groove. Thruout the order the glossae are between the paraglossae and at the distal end of the cephalic groove. They are not well-defined structures in all labia. In Chironomus (Fig. 371), they are two small membranous lobes, while in Simulium (Fig. 366), Rhabdophaga (Fig. 367), Bibio (Fig. 364), and Rhyphus (Fig. 374) they have the form of a single median membranous lobe. The glossae of Simulium are of particular interest since they have a great number of minute chitinized thickenings which radiate from the proximal end. So far as known these thickenings bear no relation to the psedotracheae of the paraglossae. The glossae of Tabanus (Fig. 391) are united and form a chitinized tridentate piece with the median tooth the longest. The glossae of Lonchoptera (Fig. 407) illustrate a form intermediate between a median spine, such as occurs in Psorophora (Fig. 381), Aphiochaeta (Fig. 393), Empis (Fig. 422), and Exoprosopa (Fig. 426), and the U-shaped structure characteristic of the Cyclorrhapha. The glossae of the Calyptratae resemble in general the glossae of Musca (Fig. 465). In the genera of this group the cephalic ends of the U-shaped piece are free and project cephalad from the point of attachment of the pseudotracheae. The glossae are not well defined in a few genera, Sapromyza (Fig. 410), Chyromya (Fig. 412), and Chloropisca (Fig. 431), for example, and it is impossible to differentiate the glossae from the chitinized groove of the mediproboscis and the proximal ends of the pseudotracheae. The glossae of Promachus (Fig. 379) are specialized in that they give rise to two thickenings which extend dorsad in the groove of the labium and serve as guides for the hypopharynx and galeae.

EPIPHARYNX AND HYPOPHARYNX

The anterior end of the alimentary canal of the Orthoptera and of insects in general is divided transversely into two parts, one forming the cuticular lining of the clypeus and labrum and the other the lining of the opposite side of the mouth cavity. The portion lining the clypeus and labrum is known as the epipharynx (ep), and that of the opposite side as the hypopharynx (hp). Each lining may be subdivided into several parts. These are of particular significance in a study of the epipharynx, which has a distinct chitinized mesal piece, and two lateral chitinized pieces which are situated near the clypeo-labral suture. These lateral pieces, which have been designated as tormae (to), and, so far as I know, are described here for the first time, project cephalad toward the clypeo-labral suture in Melanoplus (Fig. 515) and Gryllus (Fig. 516) and connect with both the labrum and clypeus. In Gryllus they are interpolated between the clypeus and the labrum and appear as small triangular sclerites on the cephalic aspect. The tormae of Periplaneta (Fig. 514) are not as well developed as in the above-named genera, but they are present and project toward the cephalo-lateral corners of the labrum. The caudal end of the epipharynx in many insects gives rise to long chitinized arms which have been called cornua (cu). The hypopharynx may be subdivided into a distal, unpaired, median piece, which is usually called the hypopharynx, and a proximal paired area.

The chitinized portion of the anterior end of the alimentary canal of Diptera can be homologized with the epipharynx and the hypopharynx of generalized insects. The following hypothetical epipharynx and hypopharynx (Fig. 493) and their closely associated parts have been constructed for Diptera. In the figures of the lateral views of the hypothetical type an enlarged, three-sided, chitinized tube extends caudad from the dorsal end of the hypopharynx and epipharynx. It has been called the oesophageal pump (oe. p). This is not a part of the epipharynx or of the hypopharynx, but is a modification of the pharynx, a portion of the alimentary canal. All of the chitinized parts ventrad of the membranous area at the cephalic end of the oesophageal pump belong to the epipharynx and the hypopharynx. The dorsal ends of the epipharynx and the hypopharynx are united and form a single chitinized tube, and this has been called the basipharynx (bph). Except for this union, the epipharynx and the hypopharynx are continuous chitinized pieces with lance-like distal ends. The distal portion of the epipharynx is joined to the labrum by a membrane along its lateral margin. The tormae in the hypothetical type project from the lateral margins of the epipharynx and unite with the latero-ventral portions of the fronto-clypeus (fr. c). Two projections occur at the dorsal end of the basipharynx, and these are considered homologous with the cornua (cu) of the epipharynx of generalized insects. The distal end of the hypopharynx is a free lance-like organ, and a salivary duct (s. d) enters its proximal end just dorsad of the place where it joins the labium (li). The salivary duct extends thru the hypopharynx to its distal end.

The oesophageal pump of the alimentary canal is closely associated with the epipharynx and hypopharynx in all the Nematocera and in Promachus (Fig. 517), Tabanus (Fig. 494), Leptis (Fig. 520), and Psilocephala (Fig. 533) of the Brachycera. In a majority of the above forms, the oesophageal pump is an elastic, semi-chitinized, three-sided tube with muscles connecting with each of its surfaces. A contraction of these muscles expands the tube, which upon their relaxation assumes its normal shape. In some forms, as Tabanus and Promachus, there is only one chitinized elastic surface. In a number of genera, as Chironomus (Fig. 531), Psychoda (Fig. 529), and Leptis (Fig. 520), the tube is more or less membranous and not distinctly three-sided. The oesophageal pump is wanting in all the Diptera except those named, and the membranous oesophagus connects directly with the basipharynx. The oesophageal pump shows considerable variation in its shape, position, and size, as can be seen in the figures of Bibio (Fig. 523), Rhyphus (Fig. 508) and others.

The basipharynx (bph) is interpreted as including all of the united portions of the epipharynx and the hypopharynx, but the extent of this union varies somewhat in the different genera. In a majority of the Nematocera no sutures or constrictions occur between the basipharynx and the lance-like portions of the epipharynx and the hypopharynx. Such constrictions and secondary sutures do occur in a majority of the Brachycera, as in Leptis (Fig. 520) and Promachus (Fig. 517), and in all of the Cyclorrhapha. The basipharynx (bph) varies in size and shape, as can be seen in the figures. Muscles connect with the cephalic and caudal aspects of the basipharynx, those on the cephalic aspect expanding the basipharynx and thus producing suction. This sucking apparatus is well developed in all forms which have no oesophageal pump. The chitinized projections at the dorsal end of the basipharynx, called the cornua (cu), vary in shape and size. Some are blunt, others long and narrow, as in Leptis and the Calyptratae, and still others are disk-shaped, as in Promachus (Fig. 517).

Distinct tormae (to) are present in Diptera except in a few species of the Nematocera. In all the Nematocera and in Leptis (Fig. 520), Psilocephala (Fig. 533), Platypeza (Fig. 543), Aphiochaeta (Fig. 544), Lonchoptera (Fig. 539), and Scenopinus (Fig. 538), they resemble the hypothetical type in that they join with the fronto-clypeus. In other genera the tormae have an exposed portion located ventrad of the fronto-clypeus and all connection between the fronto-clypeus and the tormae is lost, except in Simulium (Fig. 497) and Tabanus. The variations in the shape and the extent of the tormae is well illustrated by the numerous figures. The so-called fulcrum described by numerous morphologists for the Calyptratae is composed of the tormae and the basipharynx. A more or less distinct secondary suture (s. s) is shown in the drawings as separating the tormae from the basipharynx, and the broken line on the tormae indicates the place of connection of the membrane of the basiproboscis with the tormae. In figures of the Nematocera and of forms in which the tormae connect with the fronto-clypeus the broken line indicates the place of union between these parts.

The epipharynx (ep) is present and closely associated with the labrum in all Diptera having functional mouth-parts. The interrelationship between the epipharynx and the labrum has been discussed under the heading labrum. The epipharynx in a number of generalized Diptera, such as Tabanus (Fig. 494), Simulium (Fig. 497), Dixa (Fig. 501), Limnobia (Fig. 507), and Sciara (Fig. 513), resembles the hypothetical type. In the majority of the Diptera it differs from the hypothetical type in that it is completely separated from the basipharynx by a constriction or a secondary suture. This hinge in the epipharynx permits the proboscis to bend at this point when it is withdrawn into the oral cavity. The lance-like portion of the epipharynx in the Calyptratae and some other forms is completely separated from the basipharynx by the development of a special piece which is commonly called the hyoid (hy). The lance-like portion of the hypopharynx also articulates against the hyoid. The hyoid is a secondary sclerite which originated from the epipharynx or the hypopharynx and serves the purpose of keeping open the alimentary canal, which passes thru it. A structure similar to the hyoid of Musca (Fig. 600) is found in Stomoxys (Fig. 599), where a large and strong trachea-like tube extends between the dorsal ends of the lance-like portions of the epipharynx, the hypopharynx, and the basipharynx.

In size and shape the epipharynx agrees more or less closely with the labrum. The epipharynx in sucking Diptera is, as a rule, long and needle-like, while in other forms it is usually short and blunt. In many genera of the Acalyptratae it has a secondary transverse suture near its distal end, as shown in Sepsis (Fig. 583) and Eristalis (Fig. 588).

A few genera show special modifications of the epipharynx. This is particularly true of Dolichopus (Fig. 524 and 528). In this genus the epipharynx closely resembles the hypothetical type in the presence of a distinct membrane between the labrum (l) and the epipharynx (ep). The specialization of the epipharynx consists in the bifurcation of its distal end and in the presence of a long club-shaped piece which projects from its meson dorsad into the cavity formed by the basipharynx, the tormae, and the fronto-clypeus. These modifications are peculiar to species of the Dolichopodidae. The bifurcations at the distal end are of particular interest, since they have been interpreted as mandibles by Langhoffer (1888). They are much longer in some of the genera of the family than in others. The lateral and caudal views of the epipharynx and the hypopharynx of Dolichopus show clearly the relation these projections have to the other parts, and justify the interpretation here given.

The single, median, distal, lance-like portion of the hypopharynx is present in all but a few of the genera studied. The cephalic portion of the labium usually connects with the lance-like portion of the hypopharynx just ventrad of the point of entrance of the salivary duct.

In a few cases, as in Borborus (Fig. 565 and 567), the hypopharynx is completely fused with the labium, while in others, as in Euaresta (Fig. 572), it is nearly so. In a majority of the genera the secondary separation of the lance-like portion of the hypopharynx from the basipharynx corresponds with the similar separation in the epipharynx. The shape and size of the hypopharynx also vary considerably, as can be seen in the figures. In mouth-parts fitted for sucking and piercing, the hypopharynx is usually long and needle-like; while in licking forms (most Calyptratae), it is greatly reduced.

The salivary duct (s. d) enters the proximal portion of the lance-like part of the hypopharynx and in most cases it is carried as a duct or groove along the cephalic surface of that organ to the distal end. The course of this duct or groove is indicated by broken lines in the figures of the caudal aspect of the hypopharynx. The salivary duct before entering the hypopharynx is enlarged and bulb-like in many species. In Tabanus (Fig. 494) the salivary bulb (s. b) is a chitinized structure continuous with the hypopharynx, while in Promachus (Fig. 517) it is chitinized, but separated from the hypopharynx. A chitinized bulb and an enlarged membranous swelling are both present in Dolichopus (Fig. 528).

The peculiar epipharynx and hypopharynx of Olfersia (Fig. 606) can be homologized with the more common types found thruout the order. The principal difference is in the shape and position of the basipharynx, the tormae, and the hyoid. The two lance-like structures embedded in the deep membranous depression about the oral cavity are the labrum-epipharynx and the lance-like part of the hypopharynx. The long, crescent-shaped piece which extends cephalad from the proximal end of the labrum-epipharynx to the pear-shaped piece, is homologous with the hyoid (hy), and the pear-shaped piece with which the hyoid connects is composed of the tormae (to) and the basipharynx (bph). The exposed parts of the tormae in the membrane ventrad of the head are very small in this genus.

Only rudiments of mouth-parts are found in the head of Gastrophilus (Fig. 490 and 492). The anterior end of the alimentary canal is a simple chitinized tube which leads to the small opening on the ventral aspect of the head. This tube undoubtedly originated from the epipharynx and the hypopharynx. The mouth-parts are greatly reduced or wanting. It is possible that the small bulb-like structures located latero-caudad of the opening are remnants of the labium. It is impossible to homologize the other minute modifications surrounding the mouth-opening.

In the Cyrtidae, as Oncodes (Fig. 109, 486, and 487), the mouth-parts show a greater reduction than in Gastrophilus, while in species of Eulonchus (Fig. 364a) they are well developed. In Oncodes a chitinized ring is present in the membrane which covers the oral cavity, and a broad plate extends dorsad from its caudal margin, giving rise to a small membranous tube, the oesophagus, which has no opening to the exterior as far as could be determined. It is impossible to homologize the parts within the oral cavity. The ental plate which gives rise to the oesophagus, may be homologous with the basal portion of the epipharynx and the hypopharynx.

A general survey of the epipharynx and hypopharynx shows that the relationship between these parts and the head-capsule corresponds with the relationship between the mouth-parts and the head. Since the epipharynx and the hypopharynx are always connected with the labrum and the proximal part of the labium, they are projected ventrad when the labrum and labium are extruded. The interrelation of the mouth-parts and the epipharynx and hypopharynx is fixed, never changing thruout the order, no matter what specialization may take place. The especially striking feature of the epipharynx and the hpopharynx in various genera which have functional mouth-parts, is the decided similarity of the two thruout the order, as shown by the various figures. The parts undergo secondary changes in their size and shape, but in no case where the mouth-parts are functional is there an entire loss of a part, which, however, happens in many cases with the mouth-appendages. The epipharynx and hpopharynx of the Calyptratae in particular show a development of joints, secondary sclerites, and membranous areas, which permit a considerable amount of flexibility.

SUMMARY

This investigation deals with the homology of all the sclerites of the fixed and movable parts of the head of one or more representatives of fifty-three of the fifty-nine families of the Diptera of North America as listed by Aldrich. With this large series it has been possible to make clear a number of little-understood relationships and structural modifications in the head and mouth-parts, and also to point out their homology with the corresponding parts and areas in insects of other orders. The six hundred and more figures show the form and structure of all the parts for each of the families studied.

Modifications of the fixed and movable parts usually take the form of reduction, change of shape, loss of chitinization, or expansion of the membranous areas. The different parts have been discussed separately, and a hypothetical or typical form has been constructed for each part.

One of the most important conclusions concerning the generalized head-capsule relates to the position of the epicranial suture. The stem of this suture along the dorso-meson represents the line of fusion of the paired sclerites of the head, while the arms of the suture ventrad of the antennal fossae enclose the unpaired sclerites of the head. This suture resembles the epicranial suture in the immature stages and the adult forms of all the generalized members of the more common orders.

Two unpaired sclerites, front and clypeus, are enclosed by the fork of the epicranial suture, and in all but one or two genera form a continuous area called the fronto-clypeus.

The labrum is an unpaired, distinct, tongue-like structure situated ventrad of the fronto-clypeus. It is joined to the epipharynx and the resulting structure is known as the labrum-epipharynx.

The tormae are chitinized lateral pieces of the epipharynx which project cephalad and unite with the fronto-clypeus in generalized Diptera. They are also present in such generalized insects as the Orthoptera. In the more specialized Diptera the tormae are interpolated between the fronto-clypeus and the labrum, and in all but a few genera lose all connection with the chitinized portions of the fronto-clypeus. Their exposed surface is best seen from a cephalic view.

The crescent-shaped frontal suture dorsad of the antennal fossae marks the line of invagination of the ptilinum. The origin of the ptilinum has not been determined.

The vertex is the paired continuous area on the cephalic aspect of the head, and the region of the vertex ventrad and mesad of each compound eye is a gena.

The compound eyes are usually large and located on the cephalolateral aspects of the head. They show secondary sexual characters in a greater number of species than do any other of the fixed and movable parts. The three ocelli are arranged in the form of a triangle and located on the vertex dorsad of the bifurcation of the arms of the epicranial suture.

The occiput and postgenae are continuous areas of the caudal surface. The former occupies the dorsal portion and is secondarily modified about the occipital foramen to form the parocciput. The postgenae are the two areas of the ventral half, separated by a membrane in generalized forms and united ventrad of the occipital foramen in all the Brachycera and the Cyclorrhapha. They are also secondarily divided into parapostgenae along the mesal membrane.

The tentorium of generalized Diptera is represented by the usual three pairs of arms and a rudimentary body. It undergoes striking modifications, and influences to a considerable extent the detailed structure of the head. The relation between the invaginations of the tentorium and the movable appendages of the mouth, which is so important a feature of all generalized insects, is also characteristic of the members of this order.

The development of the antennae from a generalized filiform type to that found among the Cyclorrhapha can be traced on the figures.

Only a few generalized Diptera have mandibles. These are only present in the females except in Simulium, in which they are well developed in both sexes.

All Diptera having functional mouth-parts have maxillae. The maxillae of generalized Diptera resemble the maxillae of generalized insects except for the absence of palpifers and the fusion of the cardines and stipites with the head-capsule. The maxillae undergo considerable modification, and are reduced to a mere ental rod and a palpus in the Calyptratae.

The labium is the most characteristic and specialized appendage of the mouth, and shows modifications due to reduction and membranous development. The palpigers and labial palpi are always wanting. The submentum and mentum are represented by a membranous area of the caudal surface of the head. The ligula, or the movable portion of the labium, has a basal part which usually gives rise to two large bulb-like paraglossae and to glossae situated between them. The paraglossae are specialized, and have chitinized areas on their lateral and caudal surfaces and pseudotracheae on their mesal surface.

The parts of the epipharynx and the hypopharynx can be homologized with the corresponding parts in generalized insects. There is a great similarity in the form of the epipharynx and hypopharynx of all Diptera, which is especially striking when considered in connection with the modifications that have taken place in all other parts.

The various mouth-parts show striking modifications thruout the order, but all, including the epipharynx and the hypopharynx, retain their relative positions, even tho they may be extruded from the head-capsule for a considerable distance, as in some of the Calyptratae. The proboscis of the Cyclorrhapha is composed of the labium, maxillae, hypopharynx, labrum-epipharynx, and tormae. The paraglossae of the labium form the large lobes, or labellae, at its distal end.

The mouth-parts of Oncodes and Gastrophilus are not functional, and are so greatly reduced that it is difficult to homologize their parts.

BIBLIOGRAPHY*

Becher, E.

1882. Zur Kenntnis der Mundtheile der Dipteren. Denkschr. k. Akad. Wissensch., Wien, math.-naturw. Cl., 45:123-162; 4 pl.

1883. Zur Abwehr. Zool. Anz., 6:88-89.

Berlese, A.

1909. Gli Insetti loro organizzazione, sviluppo abitudini e rapporti coll'umo., 1:154-159.

Blanchard, E.

1850. De la Composition de la Bouche dans les Insectes de l'ordre des Diptères. Compt. rend. Acad. Sci. Paris, 31:424-427.

Chatin, J.

1880. Sur la Constitution de l'Armature Buccale des Tabanides. Bull. de la Soc. Philom., 4, No. 8:104.

Christophers, S. R.

*1901. The Anatomy and Histology of the Adult Female Mosquito. Reports to the Malarial Committee of the Roy. Soc. (4), 20 pp.; 6 pl. London (Harrison and Sons).

Comstoch, J. H., and Kochi, C.

1902. The Skeleton of the Heads of Insects. Am. Nat., 36:13-45; 29 fig.

Cragg, F. W.

*1912. Studies on the Mouth-parts and Sucking Apparatus in the Blood-sucking Diptera. No. 1. *Philaematomyia insignis* Austen. Sci. Mem. Med. Ind., No. 54; 15 pp.; 5 pl. Calcutta.

Dimmock, G.

1881. The Anatomy of the Mouth-parts and of the Sucking Apparatus of some Diptera. Dissertation. 50 pp.; 4 pl. Boston.

1882. Anatomy of the Mouth-parts and of the Suctorial Apparatus of Culex. Psyche, 3:231-241.

Frey, R.

1913. Über die Mundteile der Mycetophiliden, Sciariden, und Cecidomyiiden. Acta Soc. Fauna Flora Fenn., 37, No. 2. 54 pp.; 4 pl., 1 fig.

Gerstfeldt, G.

*1853. Über die Mundteile der saugenden Insekten. Dissertation. 121 pp.; 4 pl. Dorpat.

Giles, G. M.

*1905. Mouth-parts of the Biting Flies.—Preliminary Note. Jour. Trop. Med., 8:363-364. London.

---

*An asterisk indicates publications that have not been seen by the author.

1906. Mouth-parts of the Biting Flies of the Genera Stomoxys and Glossina. Jour. Trop. Med., 9:99-102, 153-156, 169-173, 182-186, 198-202, 217-219, 235-236. London.

Grünberg, K.

1906. Über blutsaugende Musciden. Zool. Anz., 30:78-93; 15 fig.

1907. Die blutsaugenden Dipteren. Leitfaden. Jena (Fischer).

Hammond, A.

1874. The Mouth of the Crane-fly. Sci.-Gossip, 1874:155-160; fig. 97-113.

Hansen, H. J.

1883. Fabrica oris dipterorum: Dipterernes Mund i anatomisk og systematisk Henseende. Kjobenhavn. pp. 1-220; pl. 5.

Harris, W. H.

1902. The Dentition of the Diptera. Jour. Quek. Micr. Club (2), 8:389-398; pl. 19, 6 fig.

Hewitt, C. G.

1907. The Structure, Development and Bionomics of the House-fly, *Musca domestica*, Linn. Part I.—Anatomy of the Fly. Quart. Jour. Micr. Sci., 51:395-448; pl. 22-26.

Hunt, G.

1856. The Proboscis of the Blow-fly. Quart. Jour. Micr. Sci., 4:238-239; 2 fig.

Kellogg, V. L.

1899. The Mouth Parts of the Nematocerous Diptera. Psyche, 8:303-306, 327-330, 346-348, 355-359, 363-365; 11 fig.

1902. The Development and Homologies of the Mouth Parts of Insects. Am. Nat., 36:683-706; 26 fig.

Kolbe, H. J.

1893. Insektenkunde. 8°, 724 pp. Berlin.

Kraepelin, K.

1882. Über die Mundwerkzeuge der saugenden Insecten. Vorläufige Mittheilung. Zool. Anz., 5:574-579; 3 fig.

1883. Zur Anatomie und Physiologie des Rüssels von Musca. Zeitschr. wiss. Zool., 39:683-719; pl. 40-41.

Kulagin, N.

1905. Der Kopfbau bei Culex und Anopheles. Zeitschr. wiss. Zool., 83:285-335; 3 pl.

Langhoffer, A.

1888. Beitrag zur Kenntnis der Mundteile der Dipteren. Dissertation. 32 pp. Jena.

1901. Mandibulae Dolichopodidarum. Verhandl. Internat. Zoologen-Congress, Berlin, 5:840-846; 4 fig.

Leon, N.

1904. Vorläufige Mitteilung über den Saugrüssel der Anopheliden. Zool. Anz., 27:730-732; 1 fig.

Lowne, B. T.

1870. The Anatomy and Physiology of the Blow-fly (*Musca vomitoria*, Linn.). 121 pp.; 10 pl.

1893. A Reply to some Observations on the Mouth-organs of the Diptera. Ann. Mag. Nat. Hist. (6), 11:182-184.

1890-95. The Anatomy, Physiology, Morphology and Development of the Blow-fly *(Calliphora erythrocephala)*. 778 pp.; 52 pl. London (R. H. Porter).

MacCloskie, G.

1880. The Proboscis of the House-fly. Am. Nat., 14:153-161; 3 fig.

1884. Kraepelin's Proboscis of Musca. Am. Nat., 18:1234-1244; 12 fig.

1888. The Poison-Apparatus of the Mosquito. Am. Nat., 22:884-888; 2 fig.

Marlatt, C. L.

1896. The Mouth-parts of Insects, with particular Reference to the Diptera and Hemiptera. Abstract, Proc. A. A. A. S., 44:154-155.

Meinert, F.

1880. Sur la Conformation de la Tête et sur l'Interpretation des Organes buccaux chez les Insectes ainsi que sur la Systématique de cet Ordre. Entom. Tidskrift., 1:147-150.

1880a. Sur la Constitution des Organes buccaux chez les Diptères. Entom. Tidskrift., 1:150-153.

1881. Fluernes Munddele Trophi Dipterorum. 91 pp.; 6 pl. Kjobenhavn.

1882. Die Mundtheile der Dipteren. Zool. Anz., 5:570-574, 599-603.

Menzbier, M. A.

*1880. Über der Kopfskelett und die Mundteile der Zweiflügler. Bull. Soc. Imp. Nat. Moscou, 55:8-71; 2 pl.

Müggenburg, F. H.

1892. Der Rüssel der Diptera pupipara. Arch. Naturg., 58:287-332; 2 pl.

Packard, A. S.

1903. A Textbook of Entomology. 8°, 715 pp. New York.

Patton, W. S., and Cragg, F. W.

1913. A Textbook of Medical Entomology. London, Madras, and Calcutta (Christian Literature Society for India).

Pazos y Caballera, F. H.

1903. Del exterior e interior del Mosquito. Apuntes sobre la Anatomie y Morfologia. Rev. Trop. Med., 4:209-218; 4 pl.

Peterson, Alvah

1915. Morphological Studies on the Head and Mouth-parts of the Thysanoptera. Ann. Ent. Soc. Amer., 8:20-67; 7 pl.

Smith, J. B.

1890. A Contribution to a Knowledge of the Mouth Parts of the Diptera. Trans. Am. Ent. Soc., 17:319-339; 22 fig.

Stephens, J. W. W., and Newstead, R.

*1907. The Anatomy of the Proboscis of Biting Flies. Ann. Trop. Med., 1:171-198; 8 pl. Liverpool.

Steinheil, A. P.

1896. Trophi of Tabanus. Studies from the Lab. Zool., Dipt., Imp. Univ. Warsaw, 1896:247-250; 2 fig.

Suffolk, W. T.

1869. On the Proboscis of the Blow-fly. Monthly Micr. Jour., 1:331-342; 4 pl.

Waterhouse, C. O.

*1893. Some Observations on the Mouth-organs of Diptera. Ann. Mag. Nat. Hist. (6), 11:45-46.

Wesché, W.

1902. Undescribed Palpi on the Proboscis of some Dipterous Flies, with Remarks on the Mouth-parts in several Families. Jour. Roy. Micr. Soc., 1902:412-416; 2 pl.

*1903. The Mouth-parts of the Tsetse-fly. Knowledge, 26:116-117; 1 fig.

1904. The Labial and Maxillary Palpi in Diptera. Trans. Linn. Soc. London, 9:219-230.

1906. The Genitalia of both Sexes in Diptera and their Relation to the Armature of the Mouth. Trans. Linn. Soc. London, 9:339-386; 8 pl.

1908. The Proboscis of the Blow-fly, *Calliphora erythrocephala.* A Study in Evolution. Jour. Quek. Micr. Club (2), 10:283-295; 2 pl.

1909. The Mouth-parts of the Nemocera and their Relations to the other Families in Diptera. Corrections and Additions to the Paper published in 1904. Jour. Roy. Micr. Soc., 1909:1-16; pl. 1-4.

1912. The Phylogeny of the Nemocera, with Notes on the Leg Bristles, Hairs and certain Mouth Glands of Diptera. Biol. Bull., 23:250-270; 1 pl.

EXPLANATION OF PLATES

ABBREVIATIONS USED

a.a	Anterior arms of the tentorium
a.e.s	Arms of the epicranial suture
a.f	Antennal fossa
al.c	Alimentary canal
ant	Antenna
ar	Arista
a.s	Antennal sclerite
bph	Basipharynx
bpr	Basiproboscis
b.t	Body of the tentorium
c	Clypeus
ca	Cardo
c.e	Compound eye
ch	Chitinized
ch.th	Chitinized thickening
c.l.s	Clypeo-labral suture
cu	Cornu
d.a	Dorsal arms of the tentorium
de	Depression
dpr	Distiproboscis
ep	Epipharynx
e.s	Epicranial suture
f	Furca, also f-1, f-2, and f-3
fa	Facet
fl	Flagellum
fr	Front
fr.c	Fronto-clypeus
fr.s	Frontal suture
g	Galea
ge	Gena
gl	Glossa
h	Hook
hp	Hypopharynx
hy	Hyoid
i.a	Invagination of the anterior arm of the tentorium
i.a.d	Invagination of the anterior and dorsal arms of the tentorium
i.d	Invagination of the dorsal arm of the tentorium
i.p	Invagination of the posterior arm of the tentorium
k	Kappa (sclerite)
l	Labrum
la	Lacinia
le	Labella
l.ep	Labrum epipharynx
lg	Ligula
li	Labium
m	Membrane
md	Mandible
me	Mentum
mpr	Mediproboscis
m.ps	Main pseudotracheae
mx	Maxilla
mx.pl	Maxillary palpus
n.s	Neck sclerite
oc	Ocellus
oc.a	Ocellar area
occ	Occiput
oe	Oesophagus
oe.p	Oesophageal pump
o.f	Occipital foramen
o.l	Oral lobe
o.s	Ocular sclerite
p.a	Posterior arms of the tentorium
pd	Pedicel
pgl	Paraglossa
po	Postgena
pocc	Parocciput
ppo	Parapostgena
pr	Proboscis

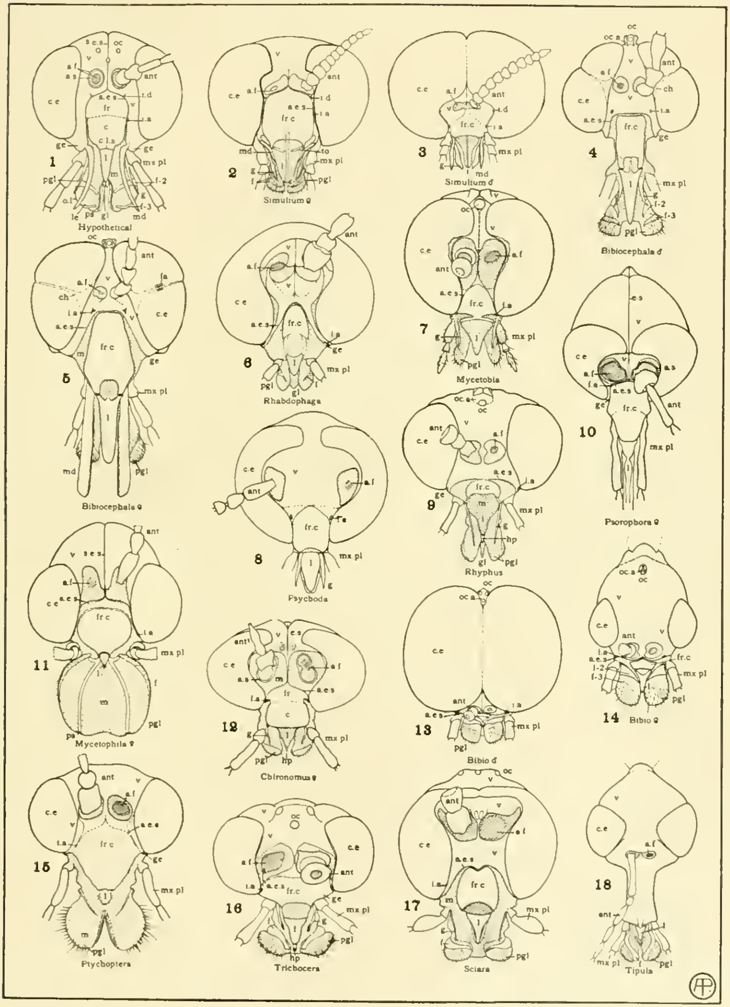
ps	Pseudotrachea
ps.th	Pseudotracheal thickening
pt	Ptilinum
r.d.a	Rudimentary dorsal arms of the tentorium
r.p.a	Rudimentary posterior arms of the tentorium
s	Suture
s.b	Salivary bulb
sc	Scape
s.d	Salivary duct
s.e.s	Stem of the epicranial suture
si	Sigma (sclerite)
so	Sense organ
s.s	Secondary suture
st	Stipes. st-1 and st-2 ectal part, st-e ental part
su	Submentum
su.me	Submentum and mentum
t	Tentorium
tee	Teeth-like structures
th	Thickening
the	Theca
to	Torma or tormae
t.th	Tentorial thickening
v	Vertex

PLATE I

EXPLANATION OF PLATE

Cephalic Aspect of the Head and Mouth-parts

Fig. 1. Hypothetical head.
Fig. 2. *Simulium venustum*, female.
Fig. 3. *Simulium johannseni*, male.
Fig. 4. *Bibiocephala elegantula*, male.
Fig. 5. *Bibiocephala elegantula*, female.
Fig. 6. *Rhabdophaga strobiloides.*
Fig. 7. *Mycetobia divergens.*
Fig. 8. *Psychoda albipennis.*
Fig. 9. *Rhyphus punctatus.*
Fig. 10. *Psorophora ciliata*, female.
Fig. 11. *Mycetophila punctata*, female.
Fig. 12. *Chironomus ferrugineovittatus*, female.
Fig. 13. *Bibio femoratus*, male.
Fig. 14. *Bibio femoratus*, female.
Fig. 15. *Ptychoptera rufocincta.*
Fig. 16. *Trichocera bimacula.*
Fig. 17. *Sciara varians.*
Fig. 18. *Tipula bicornis.*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Simulium ♂
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Rhabdophaga
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Mycetobia
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Psychoda
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Rhyphus
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Psorophora ♀
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Mycetophila ♀
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Chironomus ♀
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Bibio ♂
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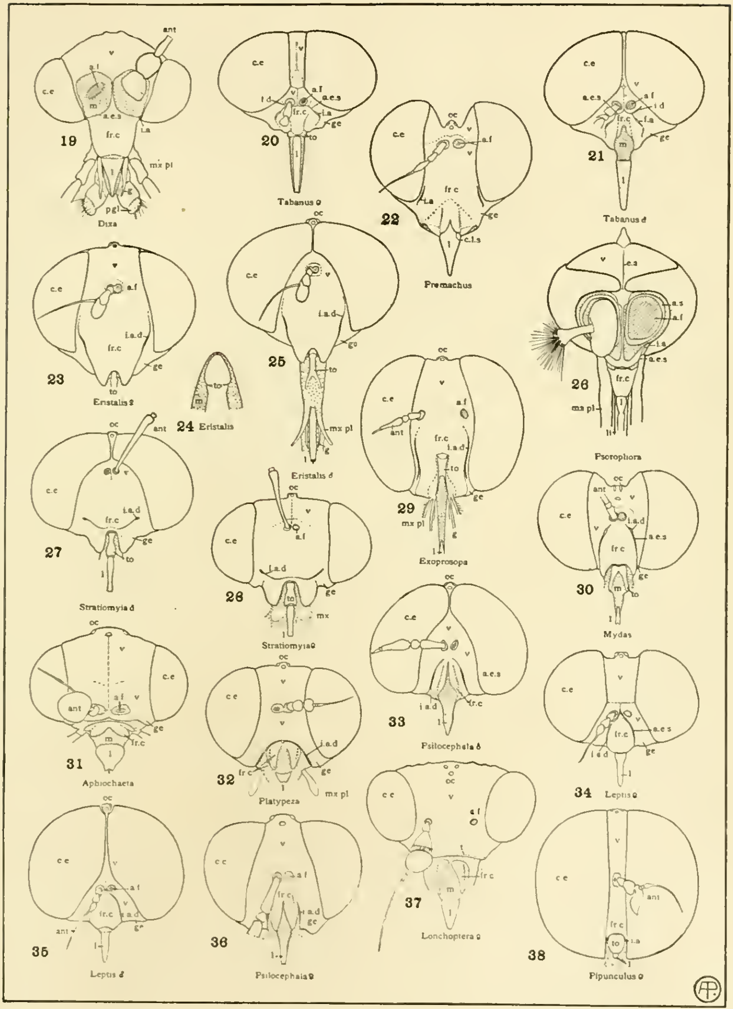
PETERSON HEAD AND MOUTH PARTS OF DIPTERA PLATE I

PLATE II

EXPLANATION OF PLATE

Cephalic aspect of the Head

Fig. 19. *Dixa clavata.*
Fig. 20. *Tabanus giganteus,* female.
Fig. 21. *Tabanus giganteus,* male.
Fig. 22. *Promachus vertebratus.*
Fig. 23. *Eristalis tenax,* female.
Fig. 24. *Eristalis tenax,* dorsal end of the tormae.
Fig. 25. *Eristalis tenax,* male.
Fig. 26. *Psorophora ciliata,* male.
Fig. 27. *Stratiomyia apicula,* male.
Fig. 28. *Stratiomyia apicula,* female.
Fig. 29. *Exoprosopa fasciata.*
Fig. 30. *Mydas clavatus.*
Fig. 31. *Aphiochaeta agarici.*
Fig. 32. *Platypeza velutina.*
Fig. 33. *Psilocephala haemorrhoidalis,* male.
Fig. 34. *Leptis vertebrata,* female.
Fig. 35. *Leptis vertebrata,* male.
Fig. 36. *Psilocephala haemorrhoidalis,* female.
Fig. 37. *Lonchoptera lutea,* female.
Fig. 38. *Pipunculus cingulatus,* female.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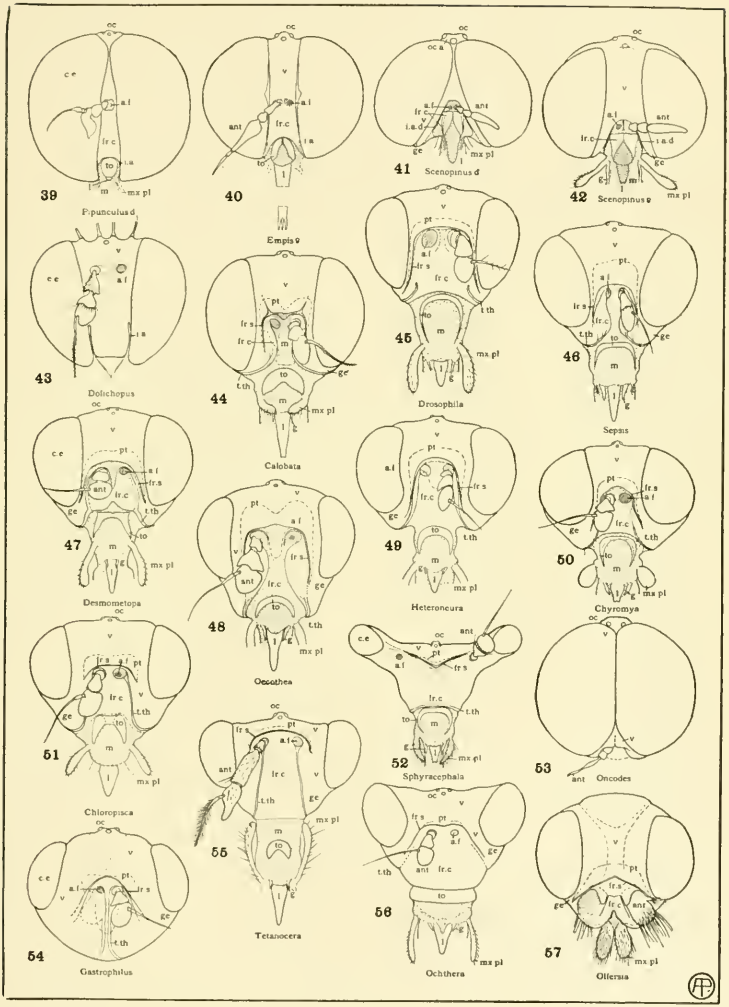
PETERSON HEAD AND MOUTH PARTS OF DIPTERA PLATE II

PLATE III

EXPLANATION OF PLATE

Cephalic Aspect of the Head

Fig. 39. *Pipunculus cingulatus,* male.
Fig. 40. *Empis clausa,* female.
Fig. 41. *Scenopinus fenestralis,* male.
Fig. 42. *Scenopinus fenestralis,* female.
Fig. 43. *Dolichopus bifractus.*
Fig. 44. *Calobata univitta.*
Fig. 45. *Drosophila ampelophila.*
Fig. 46. *Sepsis violacea.*
Fig. 47. *Desmometopa latipes.*
Fig. 48. *Oecothea fenestralis.*
Fig. 49. *Heteroneura flaviseta.*
Fig. 50. *Chyromya concolor.*
Fig. 51. *Chloropisca glabra.*
Fig. 52. *Sphyracephala brevicornis.*
Fig. 53. *Oncodes costatus.*
Fig. 54. *Gastrophilus equi.*
Fig. 55. *Tetanocera plumosa.*
Fig. 56. *Ochthera mantis.*
Fig. 57. *Olfersia ardeae.*



39 Pipunculus ♂

40 Empis ♀

41 Scenopinus ♂

42 Scenopinus ♀

43 Dolichopus

44 Calobata

45 Drosophila

46 Sepsis

47 Desmometopa

48 Oecothea

49 Heteroneura

50 Chyromya

51 Chloropisca

52 Sphyracephala

53 Oncodes

54 Gastrophilus

55 Tetanocera

56 Ochthera

57 Olfersia

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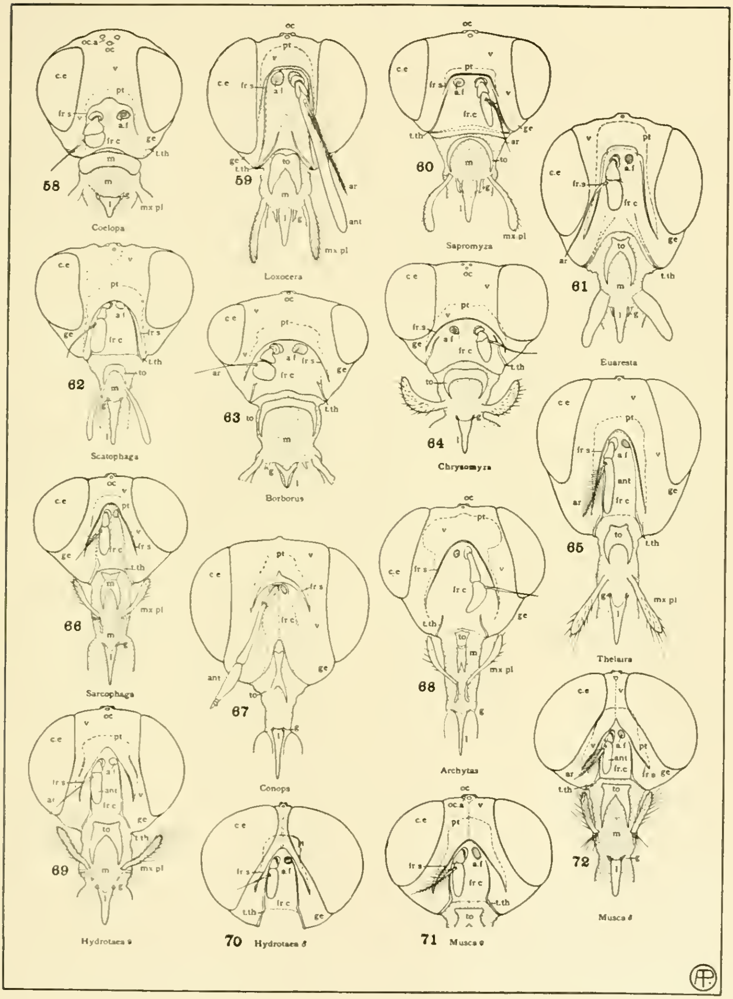
PETERSON HEAD AND MOUTH PARTS OF DIPTERA PLATE III

PLATE IV

EXPLANATION OF PLATE

CEPHALIC ASPECT OF THE HEAD

Fig. 58. *Coelopa vanduzeii.*
Fig. 59. *Loxocera pectoralis.*
Fig. 60. *Sapromyza vulgaris.*
Fig. 61. *Euaresta aequalis.*
Fig. 62. *Scatophaga furcata.*
Fig. 63. *Borborus equinus.*
Fig. 64. *Chrysomyza demandata.*
Fig. 65. *Thelairà leucozona.*
Fig. 66. *Sarcophaga haemorrhoidalis.*
Fig. 67. *Conops brachyrhynchus.*
Fig. 68. *Archytas analis.*
Fig. 69. *Hydrotaea dentipes,* female.
Fig. 70. *Hydrotaea dentipes,* male.
Fig. 71. *Musca domestica,* female.
Fig. 72. *Musca domestica,* male.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58 Coelopa

59 Loxocera

60 Sapromyza

61 Euaresta

62 Scatophaga

63 Borborus

64 Chrysomyza

65 Thelaira

66 Sarcophaga

67 Conops

68 Archytas

69 Hydrotaea ♀

70 Hydrotaea ♂

71 Musca ♀

72 Musca ♂

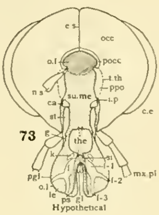
PETERSON HEAD AND MOUTH PARTS OF DIPTERA PLATE IV

PLATE V

EXPLANATION OF PLATE

Caudal Aspect of the Head

Fig. 73. Hypothetical head.
Fig. 74. *Tabanus giganteus,* female.
Fig. 75. *Tabanus giganteus,* male.
Fig. 76. *Bibiocephala elegantula,* male.
Fig. 77. *Simulium venustum,* female.
Fig. 78. *Trichocera bimacula.*
Fig. 79. *Dixa clavata.*
Fig. 80. *Rhyphus punctatus.*
Fig. 81. *Sciara varians.*
Fig. 82. *Psychoda albipennis.*
Fig. 83. *Bibiocephala elegantula,* female.
Fig. 84. *Promachus vertebratus.*
Fig. 85. *Bittacomorpha clavipes.*
Fig. 86. *Rhabdophaga strobiloides.*
Fig. 87. *Mycetophila punctata.*
Fig. 88. *Chironomus ferrugineovittatus.*
Fig. 89. *Chironomus ferrugineovittatus,* dorsal aspect.
Fig. 90. *Mycetobia divergens.*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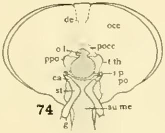
73 Hypothetical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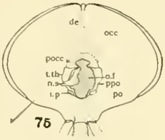
74 Tabanus ♀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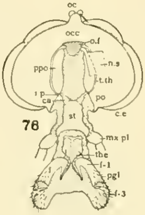
75 Tabanus ♂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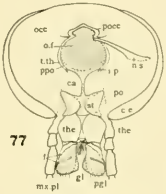
76 Bibiocephala ♂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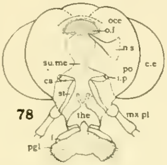
77 Simulium ♀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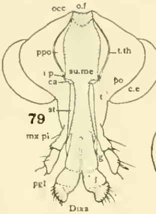
78 Trichocera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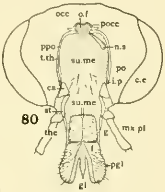
79 Dixa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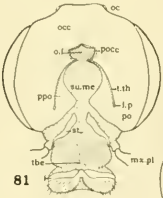
80 Rhyphus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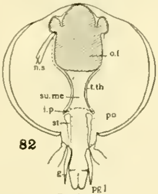
81 Sciara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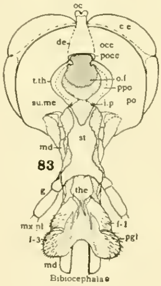
82 Psychoda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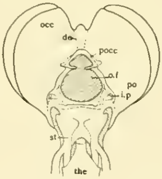
83 Bibiocephala ♀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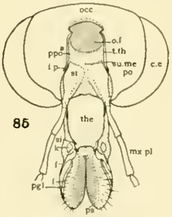
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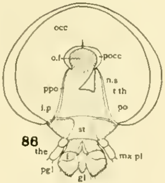
85 Bittacomorpha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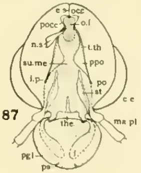
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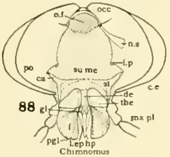
87 Mycetophila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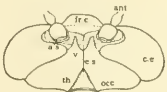
88 Chironomus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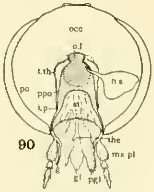
89 Chironomus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90 Mycetobia

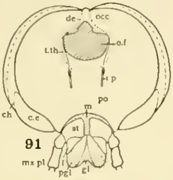
PETERSON HEAD AND MOUTH PARTS OF DIPTERA PLATE V

PLATE VI

EXPLANATION OF PLATE

Caudal Aspect of the Head

Fig. 91. *Bibio femoratus*, male.
Fig. 92. *Bibio femoratus*, female.
Fig. 93. *Limnobia immatura.*
Fig. 94. *Sphyracephala brevicornis.*
Fig. 95. *Tipula bicornis.*
Fig. 96. *Psorophora ciliata*, female.
Fig. 97. *Empis clausa*, female.
Fig. 98. *Exoprosopa fasciata.*
Fig. 99. *Mydas clavatus.*
Fig. 100. *Psilocephala haemorrhoidalis*, female.
Fig. 101. *Ochthera mantis.*
Fig. 102. *Lonchoptera lutea*, female.
Fig. 103. *Leptis vertebrata*, male.
Fig. 104. *Stratiomyia apicula*, male.
Fig. 105. *Oncodes costatus.*
Fig. 106. *Pipunculus cingulatus*, female.
Fig. 107. *Scenopinus fenestralis.*
Fig. 108. *Dolichopus* sp.
Fig. 109. *Oncodes costatus*, ventral aspect.
Fig. 110. *Platypeza velutina.*
Fig. 111. *Aphiochaeta agarici.*
Fig. 112. *Dolichopus bifractus*, lateral margins incomplete.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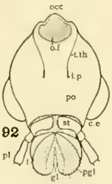
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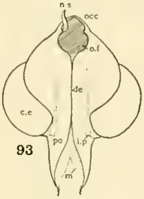
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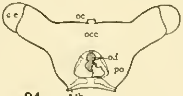
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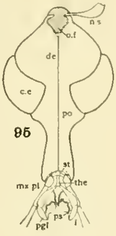
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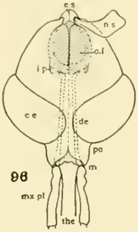
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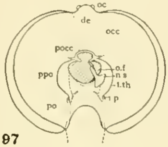
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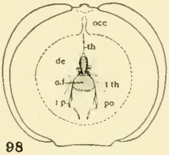
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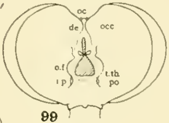
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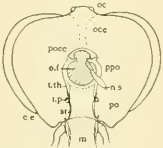
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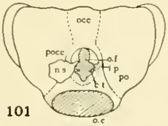
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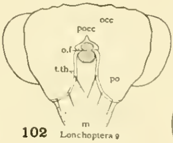
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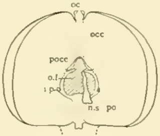
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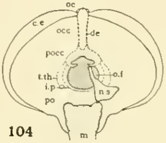
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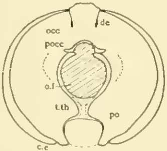
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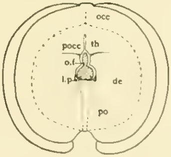
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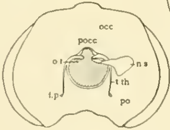
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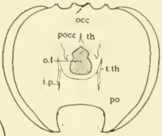
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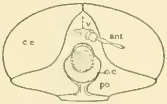
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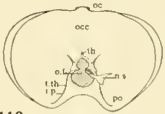
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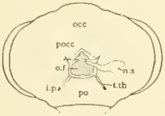
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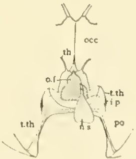
112 Dolichopus
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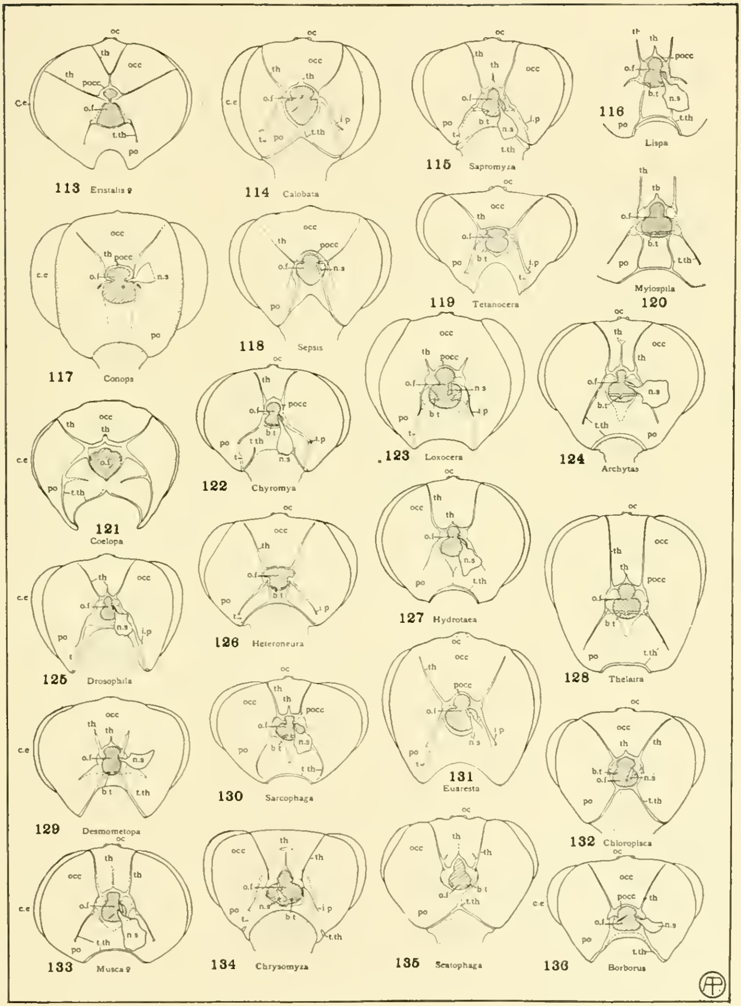
PLATE VII

EXPLANATION OF PLATE

Caudal Aspect of the Head

Fig. 113. *Eristalis tenax,* female.
Fig. 114. *Calobata univitta.*
Fig. 115. *Sapromyza vulgaris.*
Fig. 116. *Lispa nasoni,* margin incomplete.
Fig. 117. *Conops brachyrhynchus.*
Fig. 118. *Sepsis violacea.*
Fig. 119. *Tetanocera plumosa.*
Fig. 120. *Myiospila meditabunda,* margin incomplete.
Fig. 121. *Coelopa vanduzeei.*
Fig. 122. *Chiromya concolor.*
Fig. 123. *Loxocera pectoralis.*
Fig. 124. *Archytas analis.*
Fig. 125. *Drosophila ampelophila.*
Fig. 126. *Heteroneura flaviseta.*
Fig. 127. *Hydrotaea dentipes.*
Fig. 128. *Thelaira leucozona.*
Fig. 129. *Desmometopa latipes.*
Fig. 130. *Sarcophaga haemorrhoidalis.*
Fig. 131. *Euaresta aequalis.*
Fig. 132. *Chloropisca glabra.*
Fig. 133. *Musca domestica,* female.
Fig. 134. *Chrysomyza demandata.*
Fig. 135. *Scatophaga furcata.*
Fig. 136. *Borborus equinus.*



113 Eristalis ♀

114 Calobata

115 Sapromyza

116 Lispa

117 Conops

118 Sepsis

119 Tetanocera

120 Myiospila

121 Coelopa

122 Chyromya

123 Loxocera

124 Archytas

125 Drosophila

126 Heteroneura

127 Hydrotaea

128 Thelaira

129 Desmometopa

130 Sarcophaga

131 Euaresta

132 Chloropisca

133 Musca ♀

134 Chrysomyza

135 Scatophaga

136 Borborus

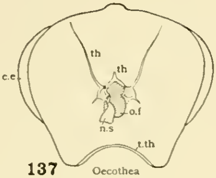
PETERSON HEAD AND MOUTH PARTS OF DIPTERA PLATE VII

PLATE VIII

EXPLANATION OF PLATE

CAUDAL AND LATERAL ASPECTS OF THE HEAD AND THE TENTORIUM

Fig. 137. *Oecothea fenestralis,* caudal aspect.
Fig. 138. *Gastrophilus equi,* caudal aspect.
Fig. 139. *Olfersia ardeae,* caudal aspect.
Fig. 140. Hypothetical head, lateral aspect.
Fig. 141. Hypothetical tentorium, lateral aspect.
Fig. 142. *Tabanus giganteus,* female, lateral aspect.
Fig. 143. *Tabanus giganteus,* lateral aspect of the tentorium.
Fig. 144. *Simulium venustum,* female, lateral aspect.
Fig. 145. *Leptis vertebrata,* male, lateral aspect.
Fig. 146. *Mydas clavatus,* lateral aspect.
Fig. 147. *Promachus vertebratus,* lateral aspect.
Fig. 148. *Promachus vertebratus,* lateral aspect of the tentorium.
Fig. 149. *Scenopinus fenestralis,* female, lateral aspect.
Fig. 150. *Sciara varians,* lateral aspect.
Fig. 151. *Pipunculus cingulatus,* lateral aspect.
Fig. 152. *Chironomus ferrugineovittatus,* lateral aspect.
Fig. 153. *Bibio femoratus,* female, lateral aspect.
Fig. 154. *Bibio femoratus,* male, lateral aspect.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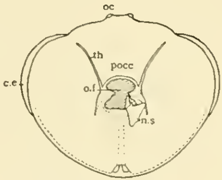
137 Oecothea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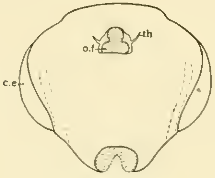
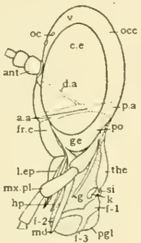
138 Gastrophilus



139 Olfersia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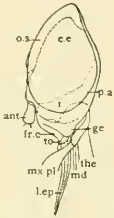
140 Hypothetical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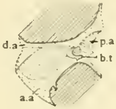
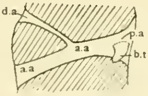
142 Tabanus ♀



Tabanus ♀
143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Hypothetical
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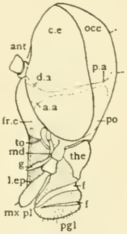
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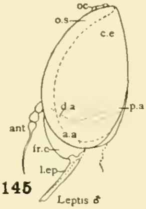
144 Simulium ♀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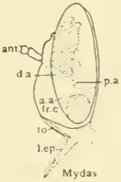
145 Leptis ♂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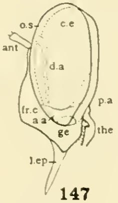
Mydas
146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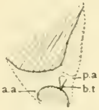
147
Promachus



Promachus
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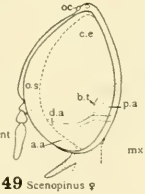
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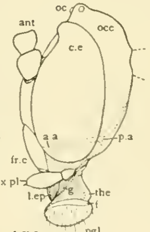
149 Scenopinus ♀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l.ep
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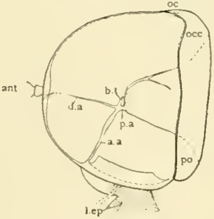
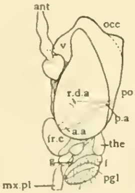
the
f
pgl

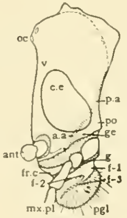
150 Sciara


oc
occ
ant
b.t
d.a
p.a
a.a
po
l.ep

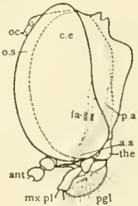
Pipunculus
151


ant
occ
v
r.d.a
po
p.a
a.a
fr.c
the
g
f
pgl
mx.pl

Chironomus
152


oc
v
c.e
p.a
po
a.a
ge
ant
g
fr.c
f-1
f-2
f-3
mx.pl
pgl

Bibio ♀
153


oc
o.s
c.e
fa-g
p.a
a.a
the
ant
mx.pl
pgl

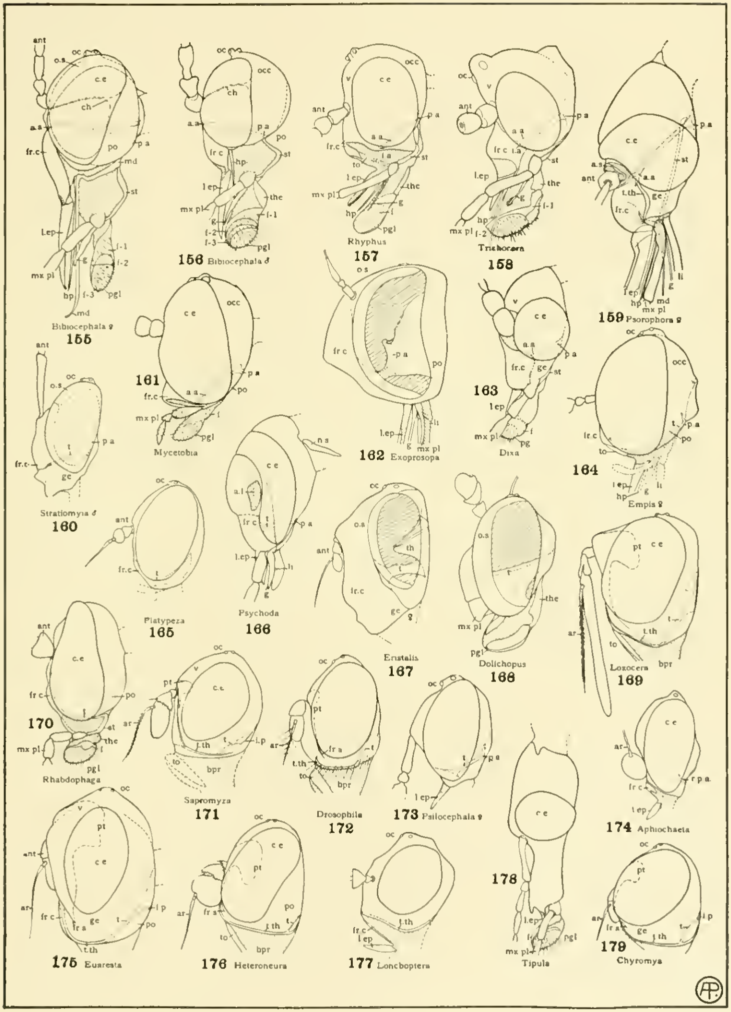
Bibio ♂
154

PLATE IX

EXPLANATION OF PLATE

LATERAL ASPECT OF THE HEAD SHOWING THE TENTORIUM

Fig. 155. *Bibiocephala elegantula,* female.
Fig. 156. *Bibiocephala elegantula,* male.
Fig. 157. *Rhyphus punctatus.*
Fig. 158. *Trichocera bimacula.*
Fig. 159. *Psorophora ciliata,* female.
Fig. 160. *Stratiomyia apicula,* male.
Fig. 161. *Mycetobia divergens.*
Fig. 162. *Exaprosopa fasciata,* eye removed.
Fig. 163. *Dixa clavata.*
Fig. 164. *Empis clausa,* female.
Fig. 165. *Platypeza velutina.*
Fig. 166. *Psychoda albipennis.*
Fig. 167. *Eristalis tenax,* female, eye removed.
Fig. 168. *Dolichopus bifractus,* eye removed.
Fig. 169. *Loxocera pectoralis.*
Fig. 170. *Rhabdophaga strobiloides.*
Fig. 171. *Sapromyza vulgaris.*
Fig. 172. *Drosophila ampelophila.*
Fig. 173. *Psilocephala haemorrhoidalis,* female.
Fig. 174. *Aphiochaeta agarici.*
Fig. 175. *Euaresta aequalis.*
Fig. 176. *Heteroneura flaviseta.*
Fig. 177. *Lonchoptera lutea.*
Fig. 178. *Tipula bicornis.*
Fig. 179. *Chyromya concolor.*


ant
o.s
oc
c.e
ch
a.a
fr.c
po
p a
md
st
l.ep
mx pl
g
hp
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f-2
f-3
pgl
occ
v
to
i.a
the
li
t.th
ge
os
n s
a.l
t
th
ar
pt
bpr
l.p
fr a

155 Bibiocephala ♀

156 Bibiocephala ♂

157 Rhyphus

158 Trichocera

159 Psorophora ♀

160 Stratiomyia ♂

161 Mycetobia

162 Exoprosopa

163 Dixa

164 Empis ♀

165 Platypeza

166 Psychoda

167 Eristalis

168 Dolichopus

169 Loxocera

170 Rhabdophaga

171 Sapromyza

172 Drosophila

173 Psilocephala ♀

174 Aphiochaeta

175 Euaresta

176 Heteroneura

177 Lonchoptera

178 Tipula

179 Chyromya

PETERSON HEAD AND MOUTH PARTS OF DIPTERA PLATE IX

PLATE X

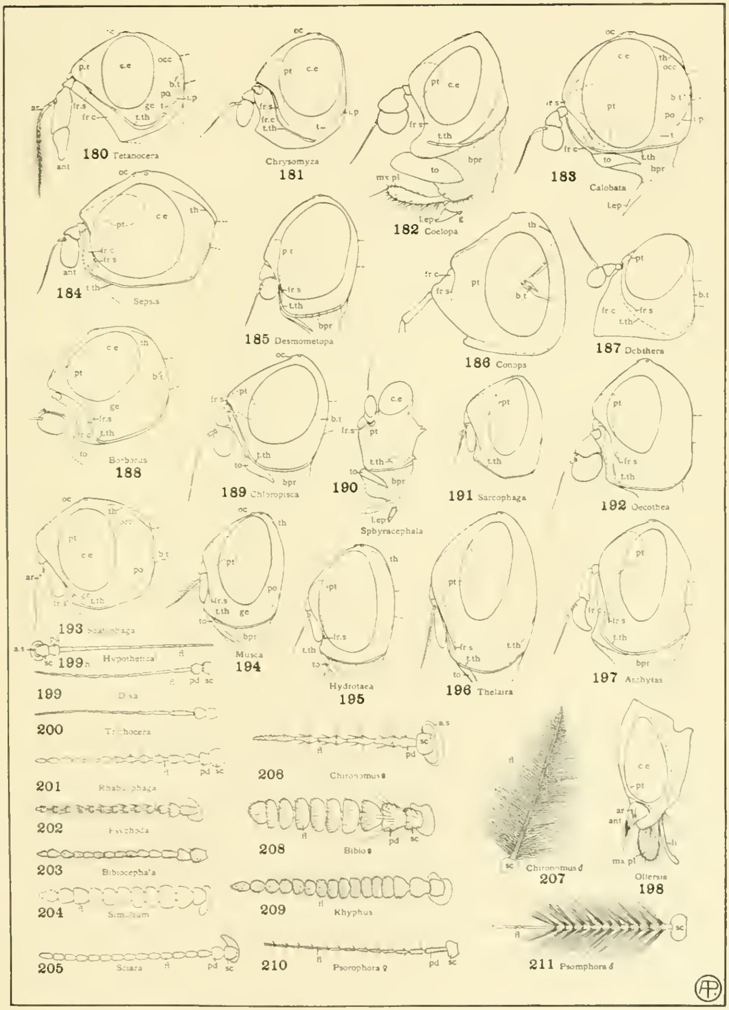
EXPLANATION OF PLATE

Lateral Aspect of the Head showing the Tentorium

Fig. 180. *Tetanocera plumosa.*
Fig. 181. *Chrysomyza demandata.*
Fig. 182. *Coelopa vanduzeii.*
Fig. 183. *Calobata univitta.*
Fig. 184. *Sepsis violacea.*
Fig. 185. *Desmometopa latipes.*
Fig. 186. *Conops brachyrhynchus.*
Fig. 187. *Ochthera mantis.*
Fig. 188. *Borborus equinus.*
Fig. 189. *Chloropisca glabra.*
Fig. 190. *Sphyracephala brevicornis.*
Fig. 191. *Sarcophaga haemorrhoidalis.*
Fig. 192. *Oecothea fenestralis.*
Fig. 193. *Scatophaga furcata.*
Fig. 194. *Musca domestica.*
Fig. 195. *Hydrotaea dentipes.*
Fig. 196. *Thelaira leucozona.*
Fig. 197. *Archytas analis.*
Fig. 198. *Olfersia ardeae.*

Antennae

Fig. 199h. Hypothetical antenna.
Fig. 199. *Dixa clavata.*
Fig. 200. *Trichocera bimacula.*
Fig. 201. *Rhabdophaga strobiloides.*
Fig. 202. *Psychoda albipennis.*
Fig. 203. *Bibiocephala elegantula.*
Fig. 204. *Simulium venustum.*
Fig. 205. *Sciara varians.*
Fig. 206. *Chironomus ferrugineovittatus*, female.
Fig. 207. *Chironomus ferrugineovittatus*, male.
Fig. 208. *Bibio femoratus*, female.
Fig. 209. *Rhyphus punctatus.*
Fig. 210. *Psorophora ciliata*, female.
Fig. 211. *Psorophora ciliata*, male.


180 Tetanocera
181 Chrysomyza
182 Coelopa
183 Calobata
184 Sepsis
185 Desmometopa
186 Conops
187 Dobthera
188 Borborus
189 Chloropisca
190 Sphyracephala
191 Sarcophaga
192 Oecothea
193 Scatophaga
194 Musca
195 Hydrotaea
196 Thelaira
197 Archytas
198 Olfersia
199a Hypotheti
199 Dixa
200 Trichocera
201 Rhabdophaga
202 Psychoda
203 Bibiocephala
204 Simulium
205 Sciara
206 Chironomus ♀
207 Chironomus ♂
208 Bibio ♀
209 Rhyphus
210 Psorophora ♀
211 Psorophora ♂
oc
occ
c.e
pt
p.t
po
b.t
l.p
t
ge
fr.s
fr.c
t.th
th
ar
ant
to
bpr
mx pl
l.ep
g
a.s
sc
pd
fl
AP

PETERSON HEAD AND MOUTH PARTS OF DIPTERA PLATE X

PLATE XI

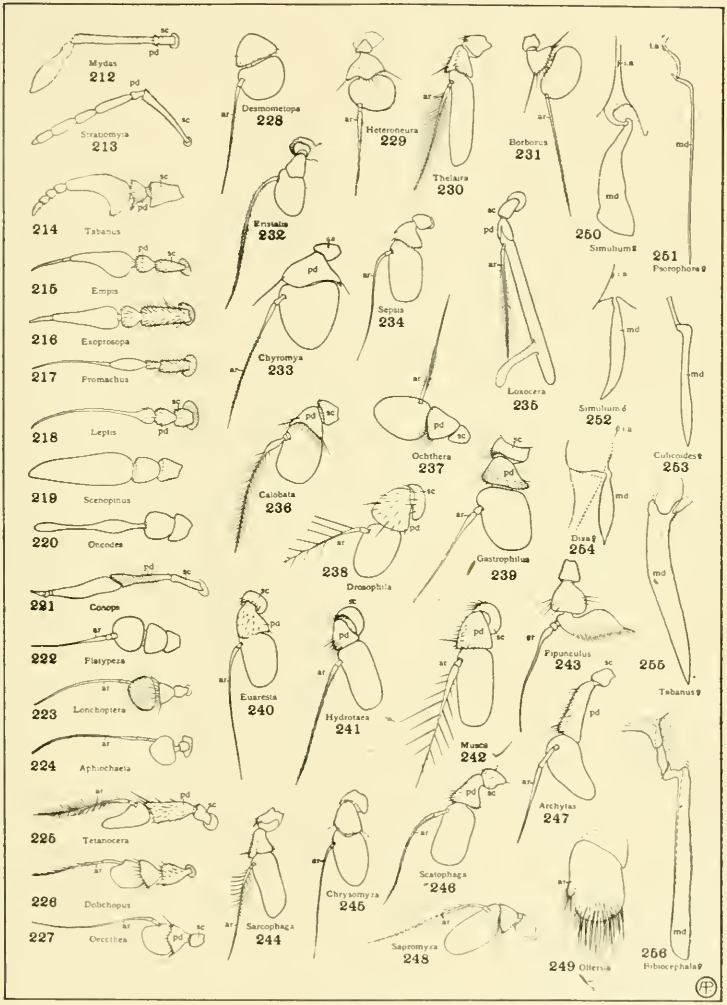
EXPLANATION OF PLATE

ANTENNAE

Fig. 212. *Mydas clavatus.*
Fig. 213. *Stratiomyia apicula.*
Fig. 214. *Tabanus giganteus.*
Fig. 215. *Empis clausa.*
Fig. 216. *Exoprosopa fasciata.*
Fig. 217. *Promachus vertebratus.*
Fig. 218. *Leptis vertebrata.*
Fig. 219. *Scenopinus fenestralis.*
Fig. 220. *Oncodes costatus.*
Fig. 221. *Conops brachyrhynchus.*
Fig. 222. *Platypeza velutina.*
Fig. 223. *Lonchoptera lutea.*
Fig. 224. *Aphiochaeta agarici.*
Fig. 225. *Tetanocera plumosa.*
Fig. 226. *Dolichopus bifractus.*
Fig. 227. *Oecothea fenestralis.*
Fig. 228. *Desmometopa latipes.*
Fig. 229. *Heteroneura flaviseta.*
Fig. 230. *Thelaira leucozona.*
Fig. 231. *Borborus equinus.*
Fig. 232. *Eristalis tenax.*
Fig. 233. *Chyromya concolor.*
Fig. 234. *Sepsis violacea.*
Fig. 235. *Loxocera pectoralis.*
Fig. 236. *Calobata univitta.*
Fig. 237. *Ochthera mantis.*
Fig. 238. *Drosophila ampelophila.*
Fig. 239. *Gastrophilus equi.*
Fig. 240. *Euaresta aequalis.*
Fig. 241. *Hydrotaea dentipes.*
Fig. 242. *Musca domestica.*
Fig. 243. *Pipunculus cingulatus.*
Fig. 244. *Sarcophaga haemorrhoidalis.*
Fig. 245. *Chrysomyza demandata.*
Fig. 246. *Scatophaga furcata.*
Fig. 247. *Archytas analis.*
Fig. 248. *Sapromyza vulgaris.*
Fig. 249. *Olfersia ardeae.*

MANDIBLES

Fig. 250. *Simulium venustum,* female.
Fig. 251. *Psorophora ciliata,* female.
Fig. 252. *Simulium johannseni,* male.
Fig. 253. *Culicoides sanguisugus,* female.
Fig. 254. *Dixa modesta,* female.
Fig. 255. *Tabanus giganteus,* female.
Fig. 256. *Bibiocephala elegantula,* female.


sc
pd
Mydas
212
pd
sc
Stratiomyia
213
sc
pd
214
Tabanus
pd
sc
215
Empis
216
Exoprosopa
217
Promachus
sc
218
Leptis
pd
219
Scenopinus
220
Oncodes
pd
sc
221
Conops
ar
222
Platypeza
ar
223
Lonchoptera
ar
224
Aphiochaeta
ar
pd
sc
225
Tetanocera
ar
226
Dolichopus
ar
pd
sc
227
Oecothea
ar
Desmometopa
228
ar
Heteroneura
229
ar
Thelaira
230
ar
Borborus
231
Eristalis
232
sc
pd
ar
Chyromya
233
ar
Sepsis
234
sc
pd
ar
Loxocera
235
pd
sc
Calobata
236
ar
pd
sc
Ochthera
237
sc
pd
ar
238
Drosophila
sc
pd
ar
Gastrophilus
239
sc
pd
ar
Euaresta
240
sc
pd
ar
Hydrotaea
241
pd
sc
ar
Musca
242
ar
Pipunculus
243
ar
Sarcophaga
244
ar
Chrysomyza
245
pd
sc
ar
Scatophaga
246
sc
pd
ar
Archytas
247
ar
Sapromyza
248
ar
249 Olfersia
l.a
md
250
Simulium ♀
l.a
md
251
Psorophora ♀
l.a
md
Simulium ♂
252
md
Culicoides ♀
253
l.a
md
Dixa ♀
254
md
255
Tabanus ♀
md
256
Bibiocephala ♀

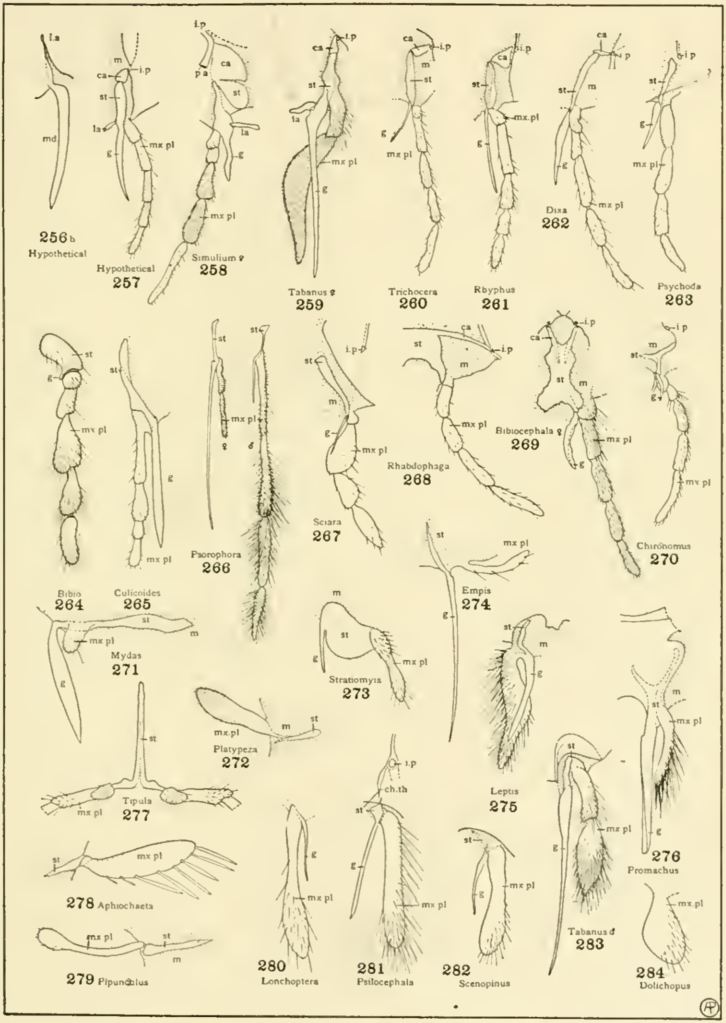
PETERSON HEAD AND MOUTH PARTS OF DIPTERA PLATE XI

PLATE XII

EXPLANATION OF PLATE

Mandible and Maxillae

Fig. 256h. Hypothetical mandible.
Fig. 257. Hypothetical maxillae.
Fig. 258. *Simulium venustum*, female, cephalic aspect.
Fig. 259. *Tabanus giganteus*, female, caudal aspect.
Fig. 260. *Trichocera bimacula*, caudal aspect.
Fig. 261. *Rhyphus punctatus*, caudal aspect.
Fig. 262. *Dixa clavata*, caudal aspect.
Fig. 263. *Psychoda albipennis*, caudal aspect.
Fig. 264. *Bibio femoratus*, caudal aspect.
Fig. 265. *Culicoides sanguisugus*, female, caudal aspect.
Fig. 266. *Psorophora ciliata*, female and male, caudal aspect.
Fig. 267. *Sciara varians*, caudal aspect.
Fig. 268. *Rhabdophaga strobiloides*, caudal aspect.
Fig. 269. *Bibiocephala elegantula*, female, caudal aspect.
Fig. 270. *Chironomus ferrugineovittatus*, cephalic aspect.
Fig. 271. *Mydas clavatus*, lateral aspect.
Fig. 272. *Platypeza velutina*, lateral aspect.
Fig. 273. *Stratiomyia apicula*, cephalic aspect.
Fig. 274. *Empis clausa*, lateral aspect.
Fig. 275. *Leptis vertebrata*, caudal aspect.
Fig. 276. *Promachus vertebratus*, caudal aspect.
Fig. 277. *Tipula bicornis*, portion of caudal aspect.
Fig. 278. *Aphiochaeta agarici*, lateral aspect.
Fig. 279. *Pipunculus cingulatus*, lateral aspect.
Fig. 280. *Lonchoptera lutea*.
Fig. 281. *Psilocephala haemorrhoidalis*, cephalic aspect.
Fig. 282. *Scenopinus fenestralis*.
Fig. 283. *Tabanus giganteus*, male, caudal aspect.
Fig. 284. *Dolichopus bifractus*.


256b Hypothetical
257 Hypothetical
258 Simulium ♀
259 Tabanus ♀
260 Trichocera
261 Rhyphus
262 Dixa
263 Psychoda
264 Bibio
265 Culicoides
266 Psorophora
267 Sciara
268 Rhabdophaga
269 Bibiocephala ♀
270 Chironomus
271 Mydas
272 Platypeza
273 Stratiomyis
274 Empis
275 Leptis
276 Promachus
277 Tipula
278 Aphiochaeta
279 Pipunculus
280 Lonchoptera
281 Psilocephala
282 Scenopinus
283 Tabanus ♂
284 Dolichopus
l.a
md
m
ca
i.p
st
la
g
mx pl
p a
ch.th

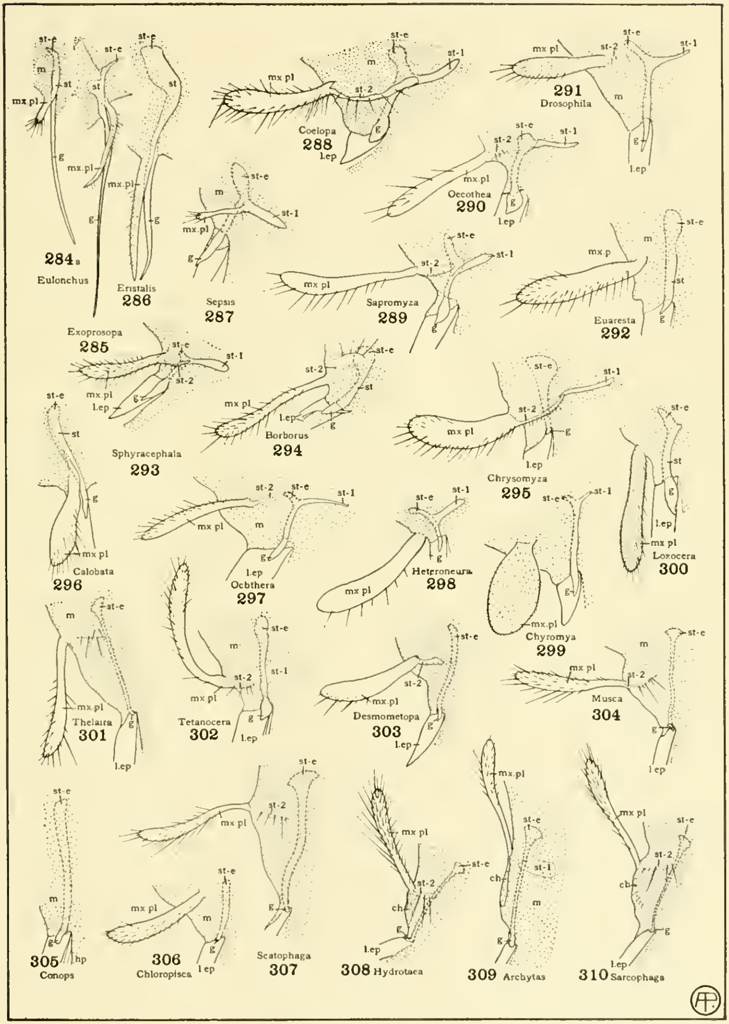
PETERSON HEAD AND MOUTH PARTS OF DIPTERA PLATE XII

PLATE XIII

EXPLANATION OF PLATE

Maxillae

Fig. 284a. *Eulonchus tristis.*
Fig. 285. *Exoprosopa fasciata.*
Fig. 286. *Eristalis tenax.*
Fig. 287. *Sepsis violacea.*
Fig. 288. *Coelopa vanduzeii.*
Fig. 289. *Sapromyza vulgaris.*
Fig. 290. *Oecothea fenestralis.*
Fig. 291. *Drosophila ampelophila.*
Fig. 292. *Euaresta aequalis.*
Fig. 293. *Sphyracephala brevicornis.*
Fig. 294. *Borborus equinus.*
Fig. 295. *Chrysomyza demandata.*
Fig. 296. *Calobata univitta.*
Fig. 297. *Ochthera mantis.*
Fig. 298. *Heteroneura flaviseta.*
Fig. 299. *Chyromya concolor.*
Fig. 300. *Loxocera pectoralis.*
Fig. 301. *Thelaira leucozona.*
Fig. 302. *Tetanocera plumosa.*
Fig. 303. *Desmometopa latipes.*
Fig. 304. *Musca domestica.*
Fig. 305. *Conops brachyrhynchus.*
Fig. 306. *Chloropisca glabra.*
Fig. 307. *Scatophaga furcata.*
Fig. 308. *Hydrotaea dentipes.*
Fig. 309. *Archytas analis.*
Fig. 310. *Sarcophaga haemorrhoidalis.*


284a
Eulonchus
285
Exoprosopa
286
Eristalis
287
Sepsis
288
Coelopa
289
Sapromyza
290
Oecothea
291
Drosophila
292
Euaresta
293
Sphyracephala
294
Borborus
295
Chrysomyza
296
Calobata
297
Ocbthera
298
Heteroneura
299
Chyromya
300
Loxocera
301
Thelaira
302
Tetanocera
303
Desmometopa
304
Musca
305
Conops
306
Chloropisca
307
Scatophaga
308
Hydrotaea
309
Archytas
310
Sarcophaga
st-e
st-1
st-2
st
m
mx pl
g
l.ep
ch
hp

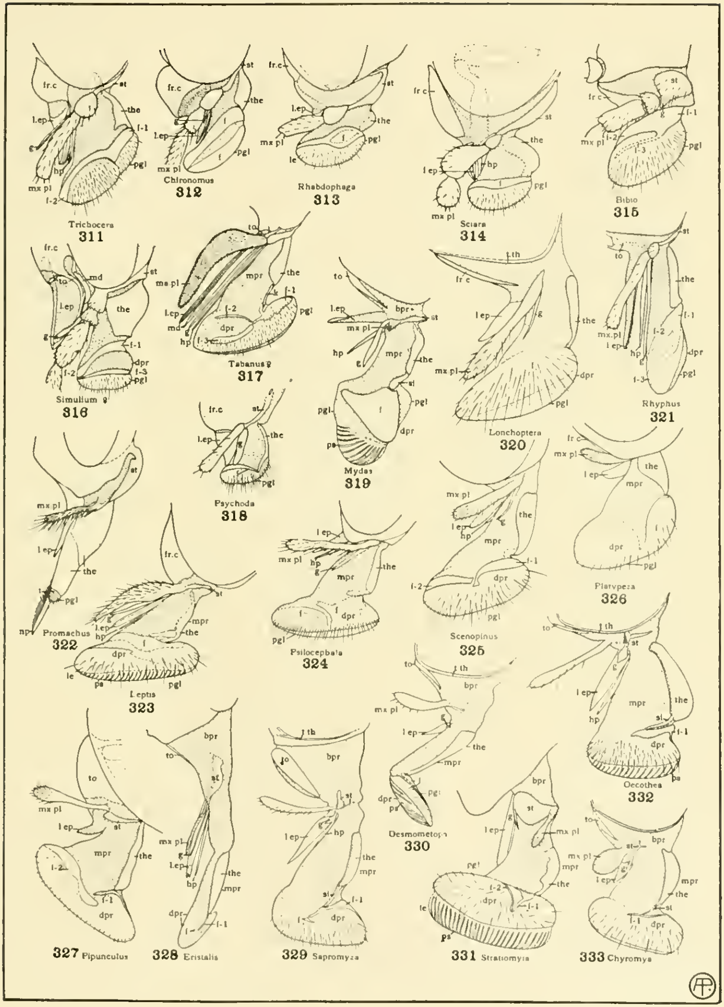
PETERSON HEAD AND MOUTH PARTS OF DIPTERA PLATE XIII

PLATE XIV

EXPLANATION OF PLATE

Lateral Aspect of the Mouth-parts or Proboscis

Fig. 311. *Trichocera bimacula.*
Fig. 312. *Chironomus ferrugineovittatus.*
Fig. 313. *Rhabdophaga strobiloides.*
Fig. 314. *Sciara varians.*
Fig. 315. *Bibio femoratus.*
Fig. 316. *Simulium venustum,* female.
Fig. 317. *Tabanus giganteus,* female.
Fig. 318. *Psychoda albipennis.*
Fig. 319. *Mydas clavatus.*
Fig. 320. *Lonchoptera lutea.*
Fig. 321. *Rhyphus punctatus.*
Fig. 322. *Promachus vertebratus.*
Fig. 323. *Leptis vertebrata.*
Fig. 324. *Psilocephala haemorrhoidalis.*
Fig. 325. *Scenopinus fenestralis.*
Fig. 326. *Platypeza velutina.*
Fig. 327. *Pipunculus cingulatus.*
Fig. 328. *Eristalis tenax.*
Fig. 329. *Sapromyza vulgaris.*
Fig. 330. *Desmometopa latipes.*
Fig. 331. *Stratiomyia apicula.*
Fig. 332. *Oecothea fenestralis.*
Fig. 333. *Chyromya concolor.*


Trichocera
311
Chironomus
312
Rhabdophaga
313
Sciara
314
Bibio
315
Simulium ♀
316
Tabanus ♀
317
Psychoda
318
Mydas
319
Lonchoptera
320
Rhyphus
321
Promachus
322
Leptis
323
Psilocephala
324
Scenopinus
325
Platypeza
326
327 Pipunculus
328 Eristalis
329 Sapromyza
Desmometopa
330
331 Stratiomyia
Oecothea
332
333 Chyromya
fr.c
st
the
f-1
f-2
f-3
l.ep
g
hp
mx pl
pgl
md
to
mpr
dpr
bpr
th
le
ps
np

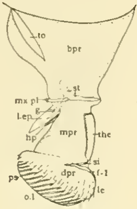
PETERSON HEAD AND MOUTH PARTS OF DIPTERA PLATE XIV

PLATE XV

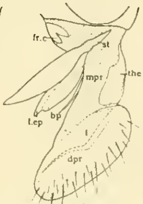
EXPLANATION OF PLATE

LATERAL ASPECT OF THE PROBOSCIS

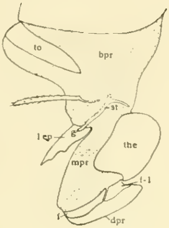
Fig. 334. *Sepsis violacea.*
Fig. 335. *Aphiochaeta agarici.*
Fig. 336. *Ochthera mantis.*
Fig. 337. *Coelopa vanduzeei.*
Fig. 338. *Sphyrocephala brevicornis.*
Fig. 339. *Loxocera pectoralis.*
Fig. 340. *Heteroneura flaviseta.*
Fig. 341. *Chrysomyza demandata.*
Fig. 342. *Borborus equinus.*
Fig. 343. *Drosophila ampelophila.*
Fig. 344. *Tetanocera plumosa.*
Fig. 345. *Chloropisca glabra.*
Fig. 346. *Thelaira leucozona.*
Fig. 347. *Euaresta aequalis.*
Fig. 348. *Calobata univitta.*
Fig. 349. *Hydrotaea dentipes.*


to
bpr
st
mx pl
g
l.ep
hp
mpr
the
si
f-1
ps
dpr
le
o.l

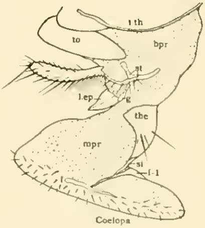
Sepsis
334


fr.c
st
mpr
the
l.ep
bp
f
dpr

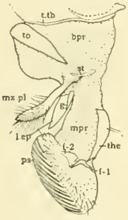
Aphiochaeta
335


to
bpr
st
l.ep
g
the
mpr
f-1
f
dpr

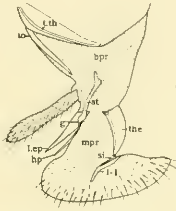
Ochthera
336


t.th
to
bpr
st
l.ep
g
the
mpr
si
f-1
f

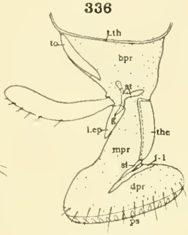
Coelopa
337


t.th
to
bpr
st
mx pl
g
mpr
l.ep
f-2
the
ps
f-1

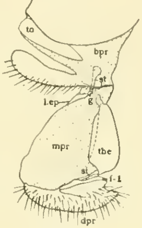
Sphyracephala
338


t.th
to
bpr
st
g
the
l.ep
hp
mpr
si
f-1

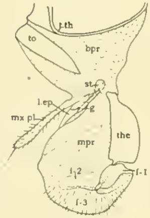
Loxocera
339


t.th
to
bpr
st
l.ep
g
the
mpr
f-1
si
dpr
ps

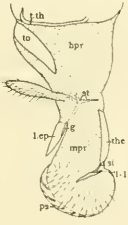
Heteroneura
340


to
bpr
st
l.ep
g
mpr
the
si
f-1
dpr

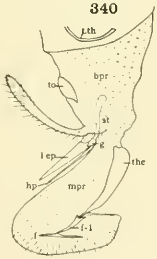
Chrysomyza
341


t.th
to
bpr
st
l.ep
g
mx pl
mpr
the
f-2
f-1
f-3

Borborus
342


t.th
to
bpr
st
l.ep
g
the
mpr
si
f-1
ps

Drosophila
343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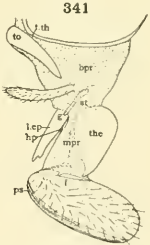
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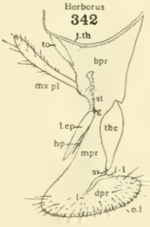
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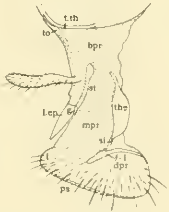
346 Thelaira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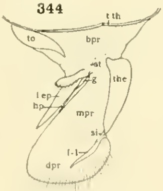
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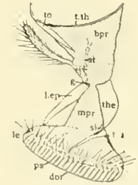
348 Calobata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349 Hydrotaea

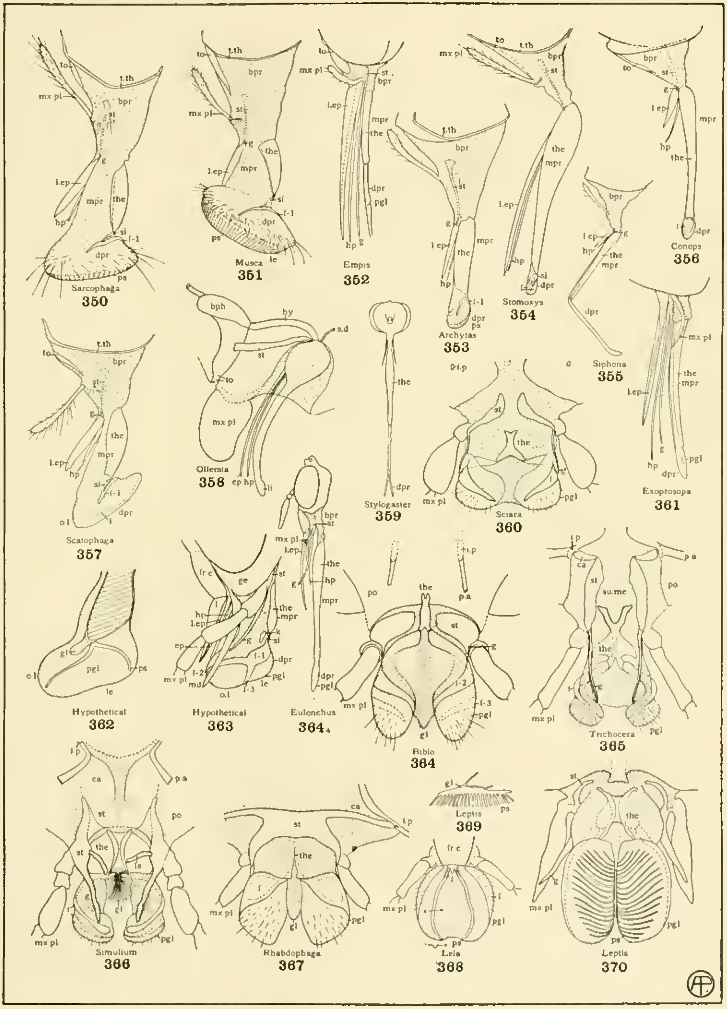
PETERSON HEAD AND MOUTH PARTS OF DIPTERA PLATE XV

PLATE XVI

EXPLANATION OF PLATE

Mouth-parts

Fig. 350. *Sarcophaga haemorrhoidalis*, lateral aspect.
Fig. 351. *Musca domestica*, lateral aspect.
Fig. 352. *Empis clausa*, lateral aspect.
Fig. 353. *Archytas analis*, lateral aspect.
Fig. 354. *Stomoxys calcitrans*, lateral aspect.
Fig. 355. *Siphona geniculata*, lateral aspect.
Fig. 356. *Conops brachyrhynchus*, lateral aspect.
Fig. 357. *Scatophaga furcata*, lateral aspect.
Fig. 358. *Olfersia ardeae*, lateral aspect.
Fig. 359. *Stylogaster biannulata*, caudal aspect.
Fig. 360. *Sciara varians*, maxillae and labium, cephalic aspect.
Fig. 361. *Exoprosopa fasciata*, lateral aspect.
Fig. 362. Hypothetical and typical labium, mesal aspect.
Fig. 363. Hypothetical mouth-parts, lateral aspect.
Fig. 364. *Bibio femoratus*, maxillae and labium, cephalic aspect.
Fig. 364a. *Eulonchus tristis*, head and mouth-parts, lateral aspect.
Fig. 365. *Trichocera bimacula*, maxillae and labium, cephalic aspect.
Fig. 366. *Simulium venustum*, maxillae and labium, cephalic aspect.
Fig. 367. *Rhabdophaga strobiloides*, maxillae and labium, caudal aspect
Fig. 368. *Leia oblectabilis*, maxillae and labium, cephalic aspect.
Fig. 369. *Leptis vertebrata*, mesal aspect of glossa.
Fig. 370. *Leptis vertebrata*, maxillae and labium, caudal aspect.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Olfersia
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Stylogaster
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Sciara
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Exoprosopa
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Hypothetical
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Hypothetical
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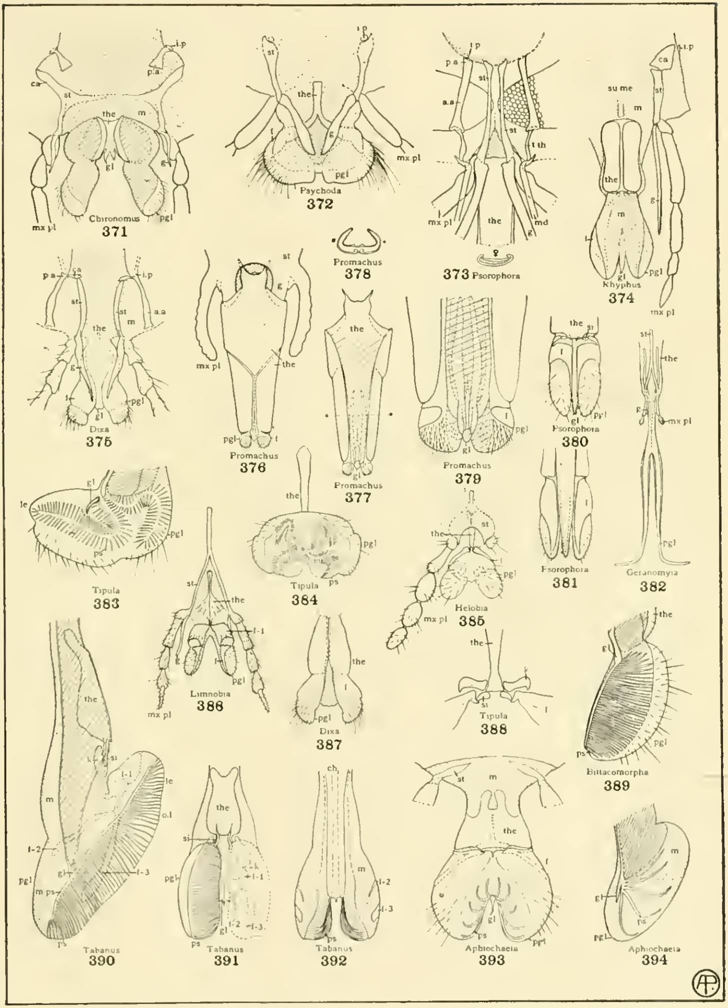
PETERSON HEAD AND MOUTH PARTS OF DIPTERA PLATE XVI

PLATE XVII

EXPLANATION OF PLATE

Maxillae and Labium

Fig. 371. *Chironomus ferrugineovittatus*, cephalic aspect.
Fig. 372. *Psychoda albipennis*, cephalic aspect.
Fig. 373. *Psorophora ciliata*, female, portions of mandibles, maxillae, labium, tentorium, and head-capsule.
Fig. 374. *Rhyphus punctatus*, cephalic aspect.
Fig. 375. *Dixa clavata*, cephalic aspect.
Fig. 376. *Promachus vertebratus*, caudal aspect.
Fig. 377. *Promachus vertebratus*, labium, cephalic aspect.
Fig. 378. *Promachus vertebratus*, cross-section of labium, see figure 377.
Fig. 379. *Promachus vertebratus*, distal end of labium, cephalic aspect.
Fig. 380. *Psorophora ciliata*, distal end of labium, caudal aspect.
Fig. 381. *Psorophora ciliata*, distal end of labium, cephalic aspect.
Fig. 382. *Geranomyia canadensis*, cephalic aspect.
Fig. 383. *Tipula bicornis*, distal end of labium, mesal aspect.
Fig. 384. *Tipula bicornis*, caudal aspect of labium.
Fig. 385. *Helobia punctipennis*, caudal aspect.
Fig. 386. *Limnobia immatura*, caudal aspect.
Fig. 387. *Dixa clavata*, caudal aspect of labium.
Fig. 388. *Tipula bicornis*, sclerites about distal end of theca of labium.
Fig. 389. *Bittacomorpha clavipes*, distal end of labium, mesal aspect.
Fig. 390. *Tabanus giganteus*, mesal aspect of labium.
Fig. 391. *Tabanus giganteus*, caudal aspect of labium.
Fig. 392. *Tabanus giganteus*, cephalic aspect of labium.
Fig. 393. *Aphiochaeta agarici*, caudal aspect.
Fig. 394. *Aphiochaeta agarici*, distal end of labium, mesal aspect.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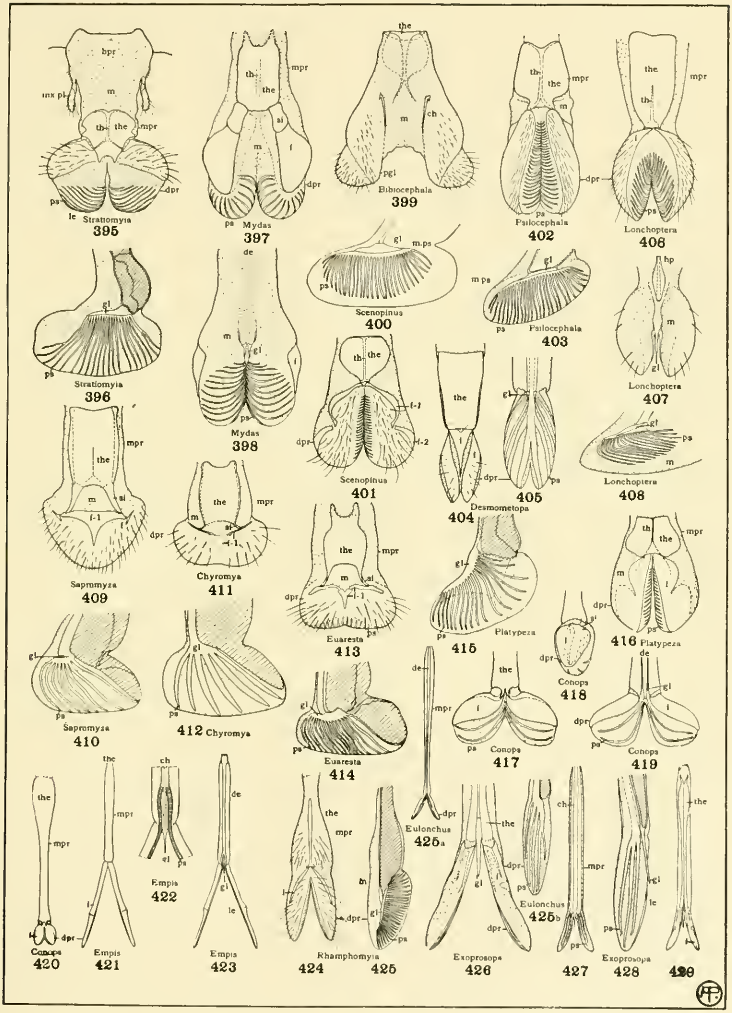
PETERSON HEAD AND MOUTH PARTS OF DIPTERA PLATE XVII

PLATE XVIII

EXPLANATION OF PLATE

Labium

Fig. 395. *Stratiomyia apicula*, caudal aspect of proboscis.
Fig. 396. *Stratiomyia apicula*, mesal aspect.
Fig. 397. *Mydas clavatus*, caudal aspect.
Fig. 398. *Mydas clavatus*, cephalic aspect.
Fig. 399. *Bibiocephala elegantula*, cephalic aspect.
Fig. 400. *Scenopinus fenestralis*, mesal aspect.
Fig. 401. *Scenopinus fenestralis*, caudal aspect.
Fig. 402. *Psilocephala haemorrhoidalis*, caudal aspect.
Fig. 403. *Psilocephala haemorrhoidalis*, mesal aspect.
Fig. 404. *Desmometopa latipes*, caudal aspect.
Fig. 405. *Desmometopa latipes*, cephalic aspect.
Fig. 406. *Lonchoptera lutea*, caudal aspect.
Fig. 407. *Lonchoptera lutea*, cephalic aspect.
Fig. 408. *Lonchoptera lutea*, mesal aspect.
Fig. 409. *Sapromyza vulgaris*, caudal aspect.
Fig. 410. *Sapromyza vulgaris*, mesal aspect.
Fig. 411. *Chyromya concolor*, caudal aspect.
Fig. 412. *Chyromya concolor*, mesal aspect.
Fig. 413. *Euaresta aequalis*, caudal aspect.
Fig. 414. *Euaresta aequalis*, mesal aspect.
Fig. 415. *Platypeza velutina*, mesal aspect.
Fig. 416. *Platypeza velutina*, caudal aspect.
Fig. 417. *Conops brachyrhynchus*, distal end, caudal aspect.
Fig. 418. *Conops brachyrhynchus*, distal end, lateral aspect.
Fig. 419. *Conops brachyrhynchus*, distal end, cephalic aspect.
Fig. 420. *Conops brachyrhynchus*, caudal aspect.
Fig. 421. *Empis clausa*, caudal aspect.
Fig. 422. *Empis clausa*, portion of cephalic aspect.
Fig. 423. *Empis clausa*, cephalic aspect.
Fig. 424. *Rhamphomyia glabra*, caudal aspect.
Fig. 425. *Rhamphomyia glabra*, mesal aspect.
Fig. 425a. *Eulonchus tristis*, cephalic aspect.
Fig. 425b. *Eulonchus tristis*, distal end, mesal aspect.
Fig. 426. *Exoprosopa fasciata*, distal end, caudal aspect.
Fig. 427. *Exoprosopa fasciata*, cephalic aspect.
Fig. 428. *Exoprosopa fasciata*, distal end, mesal aspect.
Fig. 429. *Exoprosopa fasciata*, caudal aspect.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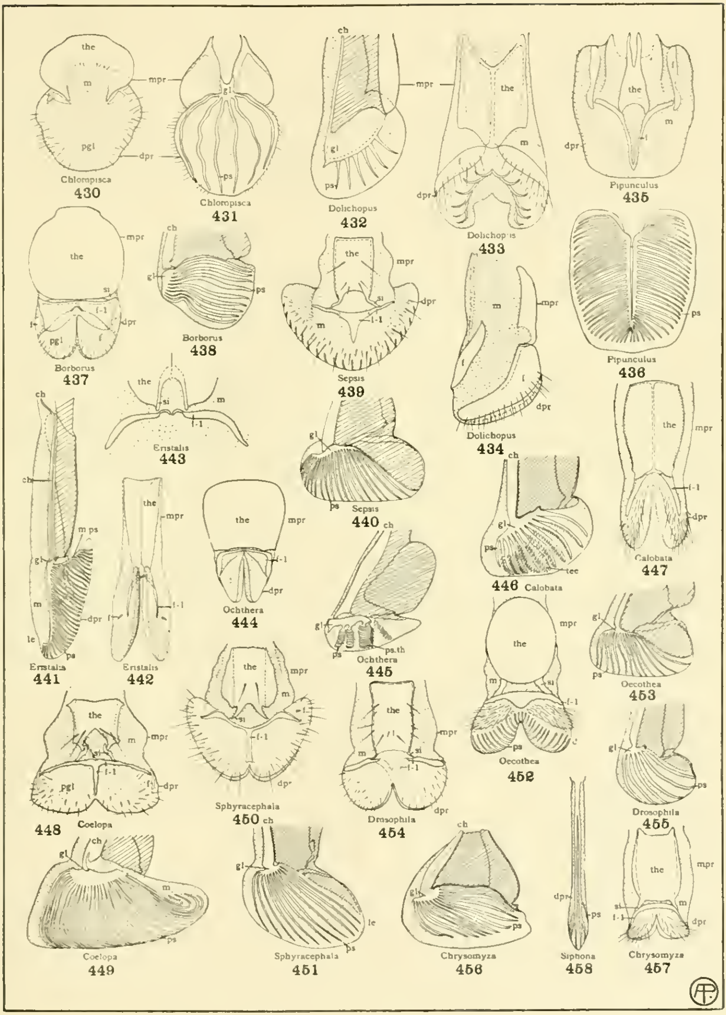
PETERSON HEAD AND MOUTH PARTS OF DIPTERA PLATE XVIII

PLATE XIX

EXPLANATION OF PLATE

LABIUM

Fig. 430. *Chloropisca glabra*, caudal aspect.
Fig. 431. *Chloropisca glabra*, cephalic aspect.
Fig. 432. *Dolichopus bifractus*, mesal aspect.
Fig. 433. *Dolichopus bifractus*, caudal aspect.
Fig. 434. *Dolichopus bifractus*, lateral aspect.
Fig. 435. *Pipunculus cingulatus*, caudal aspect.
Fig. 436. *Pipunculus cingulatus*, cephalic aspect.
Fig. 437. *Borborus equinus*, caudal aspect.
Fig. 438. *Borborus equinus*, mesal aspect.
Fig. 439. *Sepsis violacea*, caudal aspect.
Fig. 440. *Sepsis violacea*, mesal aspect.
Fig. 441. *Eristalis tenax*, mesal aspect.
Fig. 442. *Eristalis tenax*, caudal view.
Fig. 443. *Eristalis tenax*, distal end of theca, caudal aspect.
Fig. 444. *Ochthera mantis*, caudal aspect.
Fig. 445. *Ochthera mantis*, mesal aspect.
Fig. 446. *Calobata univitta*, mesal aspect.
Fig. 447. *Calobata univitta*, caudal aspect.
Fig. 448. *Coelopa vanduzeii*, caudal aspect.
Fig. 449. *Coelopa vanduzeii*, mesal aspect.
Fig. 450. *Sphyracephala brevicornis*, caudal aspect.
Fig. 451. *Sphyracephala brevicornis*, mesal aspect.
Fig. 452. *Oecothea fenestralis*, caudal aspect.
Fig. 453. *Oecothea fenestralis*, mesal aspect.
Fig. 454. *Drosophila ampelophila*, caudal aspect.
Fig. 455. *Drosophila ampelophila*, mesal aspect.
Fig. 456. *Chrysomyza demandata*, mesal aspect.
Fig. 457. *Chrysomyza demandata*, caudal aspect.
Fig. 458. *Siphona geniculata*, distal end, cephalic aspect.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Sepsis
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Dolichopus
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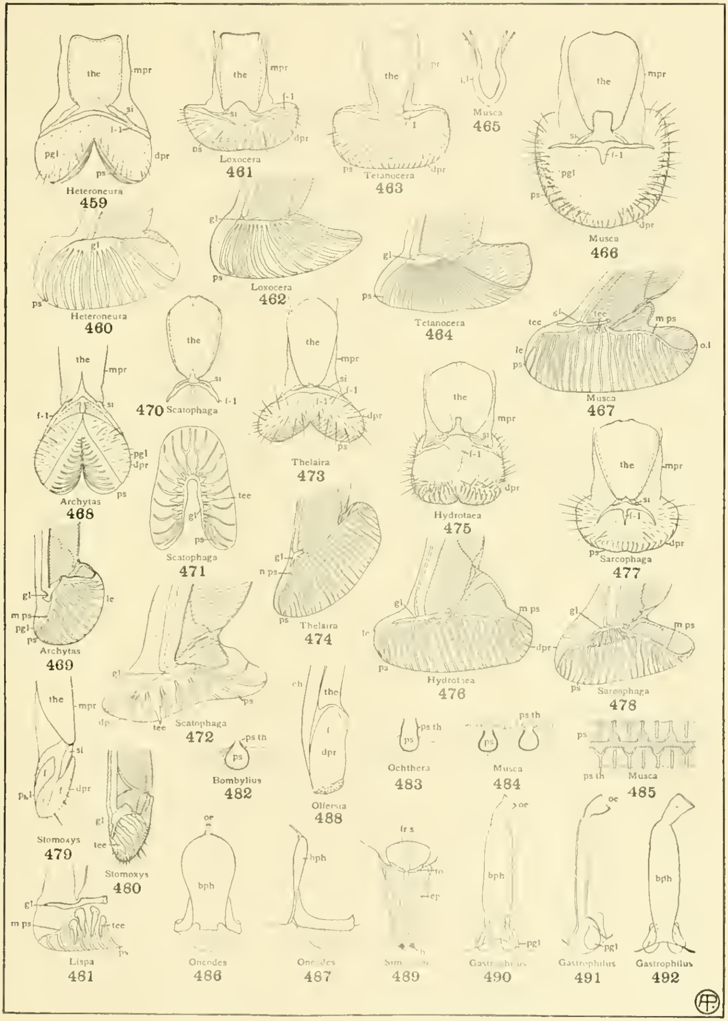
PETERSON HEAD AND MOUTH PARTS OF DIPTERA PLATE XIX

PLATE XX

EXPLANATION OF PLATE

Labium and other Parts

Fig. 459. *Heteroneura flaviseta,* caudal aspect.
Fig. 460. *Heteroneura flaviseta,* mesal aspect.
Fig. 461. *Loxocera pectoralis,* caudal aspect.
Fig. 462. *Loxocera pectoralis,* mesal aspect.
Fig. 463. *Tetanocera plumosa,* caudal aspect.
Fig. 464. *Tetanocera plumosa,* mesal aspect.
Fig. 465. *Musca domestica,* dorsal aspect of glossae.
Fig. 466. *Musca domestica,* caudal aspect.
Fig. 467. *Musca domestica,* mesal aspect.
Fig. 468. *Archytas analis,* caudal aspect.
Fig. 469. *Archytas analis,* mesal aspect.
Fig. 470. *Scatophoga furcata,* caudal aspect of mediproboscis.
Fig. 471. *Scatophaga furcata,* ventral aspect of distiproboscis.
Fig. 472. *Scatophaga furcata,* mesal aspect.
Fig. 473. *Thelaira leucozona,* caudal aspect.
Fig. 474. *Thelaira leucozona,* mesal aspect.
Fig. 475. *Hydrotaea dentipes,* caudal aspect.
Fig. 476. *Hydrotaea dentipes,* mesal aspect.
Fig. 477. *Sarcophaga haemorrhoidalis,* caudal aspect.
Fig. 478. *Sarcophaga haemorrhoidalis,* mesal aspect.
Fig. 479. *Stomoxys calcitrans,* distal end, lateral aspect.
Fig. 480. *Stomoxys calcitrans,* distal end, mesal aspect.
Fig. 481. *Lispa nasoni,* distal end, mesal aspect.
Fig. 482. *Bombylius major,* cross-section thru pseudotrachea. (After Dimmock.)
Fig. 483. *Ochthera mantis,* cross-section thru pseudotrachea.
Fig. 484. *Musca (Calliphora) vomitoria,* cross-section thru pseudotrachea (After Dimmock.)
Fig. 485. *Musca (Colliphora) vomitoria,* an enlarged pseudotrachea. (After Dimmock.)
Fig. 486. *Oncodes costatus,* entire mouth-parts, caudal aspect.
Fig. 487. *Oncodes costatus,* entire mouth-parts, lateral aspect.
Fig. 488. *Olfersia ardeae,* distal end, lateral aspect.
Fig. 489. *Simulium venustum,* cephalic aspect of the labrum.
Fig. 490. *Gastrophilus equi,* entire mouth-parts, caudal aspect.
Fig. 491. *Gastrophilus equi,* sagittal section thru mouth-parts.
Fig. 492. *Gastrophilus equi,* entire mouth-parts, cephalic aspect.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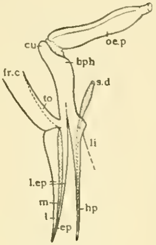
PETERSON HEAD AND MOUTH PARTS OF DIPTERA PLATE XX

PLATE XXI

EXPLANATION OF PLATE

EPIPHARYNX AND HYPOPHARYNX AND ASSOCIATED PARTS

Fig. 493. Hypothetical type, lateral aspect.
Fig. 494. *Tabanus giganteus,* female, lateral aspect.
Fig. 495. *Tabanus giganteus,* male, lateral aspect.
Fig. 496. *Tabanus giganteus,* female, caudal aspect.
Fig. 497. *Simulium venustum,* female, lateral aspect.
Fig. 498. *Simulium venustum,* female, caudal aspect.
Fig. 499. *Trichocera bimacula,* lateral aspect.
Fig. 500. *Trichocera bimacula,* caudal aspect.
Fig. 501. *Dixa clavata,* lateral aspect.
Fig. 502. *Dixa clavata,* caudal aspect.
Fig. 503. *Tipula bicornis,* lateral aspect.
Fig. 504. *Psorophora ciliata,* female, lateral aspect.
Fig. 505. *Psorophora ciliata,* female, caudal aspect.
Fig. 506. *Geranomyia canadensis,* lateral aspect.
Fig. 507. *Limnobia immatura,* lateral aspect.
Fig. 508. *Rhyphus punctatus,* lateral aspect.
Fig. 509. *Rhyphus punctatus,* caudal aspect.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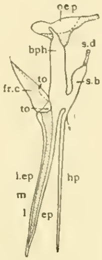
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Tabanus♀
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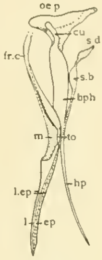
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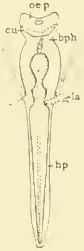
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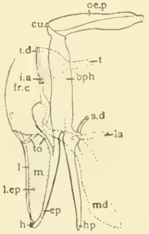
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Simulium
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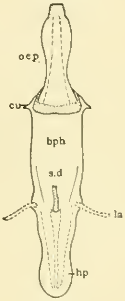
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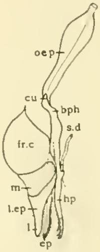
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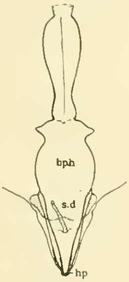

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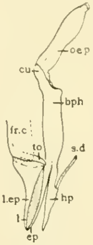
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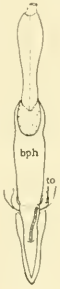

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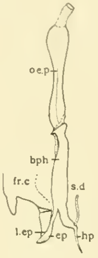
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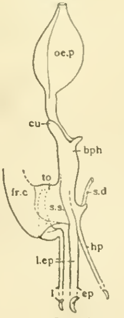
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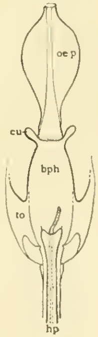
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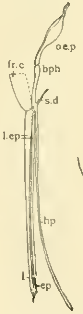
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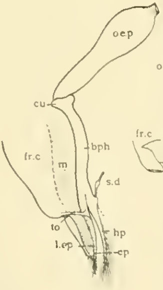
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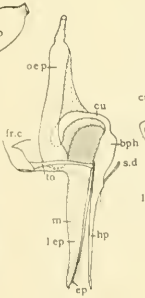
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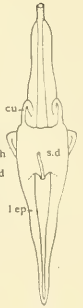


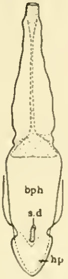
Rhyphus
509

PLATE XXII

EXPLANATION OF PLATE

Epipharynx and Hypopharynx and Associated Parts

Fig. 510. *Rhabdophaga strobiloides,* caudal aspect.
Fig. 511. *Rhabdophaga strobiloides,* lateral aspect.
Fig. 512. *Sciara varians,* caudal aspect.
Fig. 513. *Sciara varians,* lateral aspect.
Fig. 514. *Periplaneta orientalis,* clypeus, labrum, and epipharynx spread out, ental aspect.
Fig. 515. *Melanoplus differentialis,* clypeus, labrum, and epipharynx spread out, ental aspect.
Fig. 516. *Gryllus pennsylvanicus,* right-half of clypeus, labrum, and epipharynx, cephalic and caudal aspects.
Fig. 517. *Promachus vertebratus,* lateral aspect.
Fig. 518. *Promachus vertebratus,* epipharynx and labrum, caudal aspect.
Fig. 519. *Promachus vertebratus,* caudal aspect.
Fig. 520. *Leptis vertebrata,* lateral aspect.
Fig. 521. *Culicoides sanguisugus,* lateral aspect.
Fig. 522. *Bibio femoratus,* caudal aspect.
Fig. 523. *Bibio femoratus,* lateral aspect.
Fig. 524. *Dolichopus bifroctus,* caudal aspect.
Fig. 525. *Leptis vertebrata,* caudal aspect.
Fig. 526. *Bibiocephala elegantula,* caudal aspect.
Fig. 527. *Bibiocephala elegantula,* lateral aspect.
Fig. 528. *Dolichopus bifractus,* lateral aspect.



Rhabdophaga
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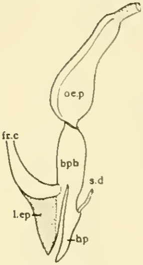
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Rhabdophaga
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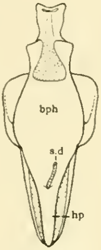

Sciara
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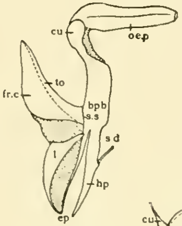
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Sciara
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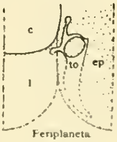

Periplaneta
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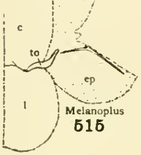

Melanoplus
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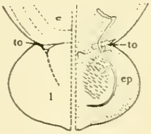

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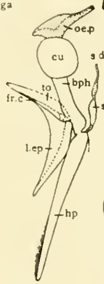
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Promachus
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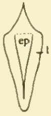

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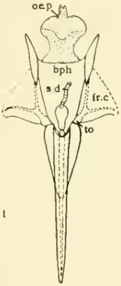
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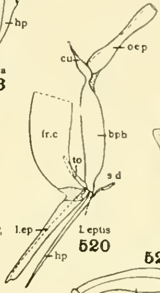
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Leptis
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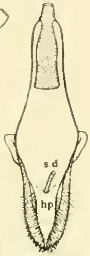
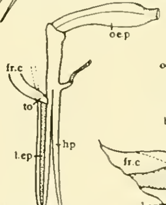


522 Bibio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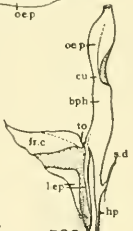
Culicoides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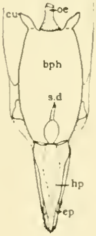
Bibio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Dolichopus
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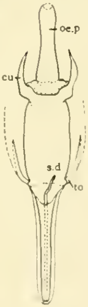

Leptis
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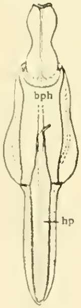

Bibiocephala
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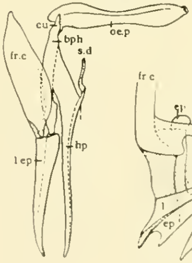
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Bibiocephala
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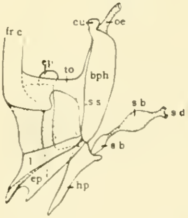
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Dolichopus
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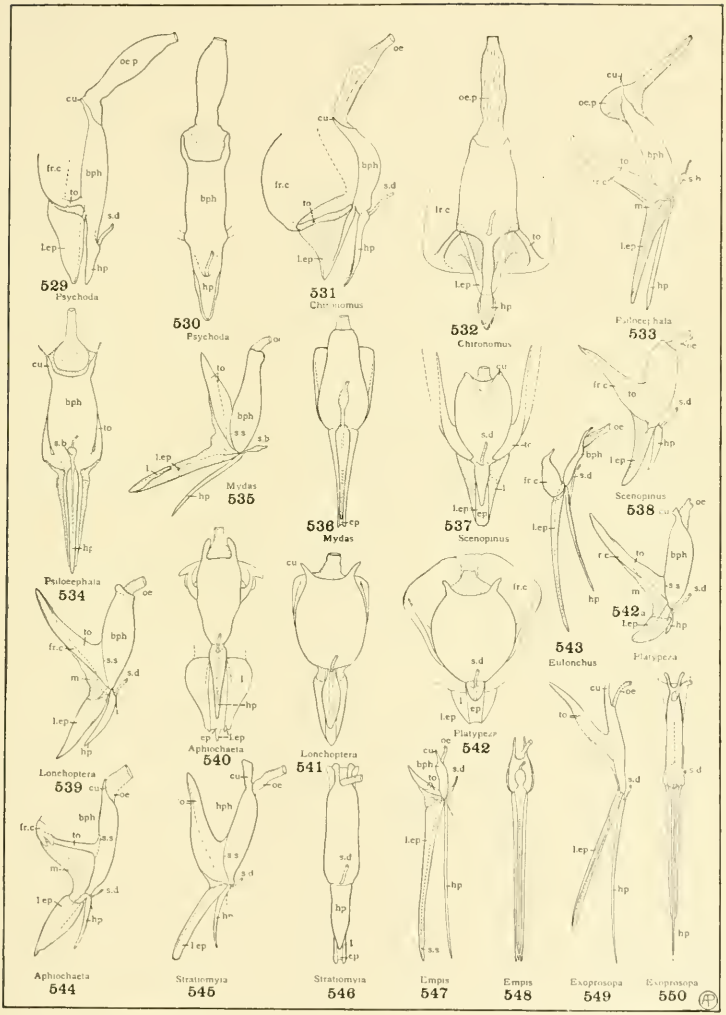
PLATE XXIII

EXPLANATION OF PLATE

Epipharynx and Hypopharynx and Associated Parts

Fig. 529. *Psychoda albipennis,* lateral aspect.
Fig. 530. *Psychoda albipennis,* caudal aspect.
Fig. 531. *Chironomus ferrugineovittatus,* lateral aspect.
Fig. 532. *Chironomus ferrugineovittatus,* caudal aspect.
Fig. 533. *Psilocephala haemorrhoidalis,* lateral aspect.
Fig. 534. *Psilocephala haemorrhoidalis,* caudal aspect.
Fig. 535. *Mydas clavatus,* lateral aspect.
Fig. 536. *Mydas clavatus,* caudal aspect.
Fig. 537. *Scenopinus fenestralis,* caudal aspect.
Fig. 538. *Scenopinus fenestralis,* lateral aspect.
Fig. 539. *Lonchoptera lutea,* lateral aspect.
Fig. 540. *Aphiochaeta agarici,* caudal aspect.
Fig. 541. *Lonchoptera lutea,* caudal aspect.
Fig. 542. *Platypeza velutina,* caudal aspect.
Fig. 542a. *Platypeza velutina,* lateral aspect.
Fig. 543. *Eulonchus tristis,* lateral aspect.
Fig. 544. *Aphiochaeta agarici,* lateral aspect.
Fig. 545. *Stratiomyia apicula,* lateral aspect.
Fig. 546. *Stratiomyia apicula,* caudal aspect.
Fig. 547. *Empis clausa,* lateral aspect.
Fig. 548. *Empis clausa,* caudal aspect.
Fig. 549. *Exoprosopa fasciata,* lateral aspect.
Fig. 550. *Exoprosopa fasciata,* caudal aspect.



529 Psychoda

530 Psychoda

531 Chironomus

532 Chironomus

533 Psilocephala

534 Psilocephala

535 Mydas

536 Mydas

537 Scenopinus

538 Scenopinus

539 Lonchoptera

540 Aphiochaeta

541 Lonchoptera

542 Platypeza

542a Platypeza

543 Eulonchus

544 Aphiochaeta

545 Stratiomyia

546 Stratiomyia

547 Empis

548 Empis

549 Exoprosopa

550 Exoprosopa

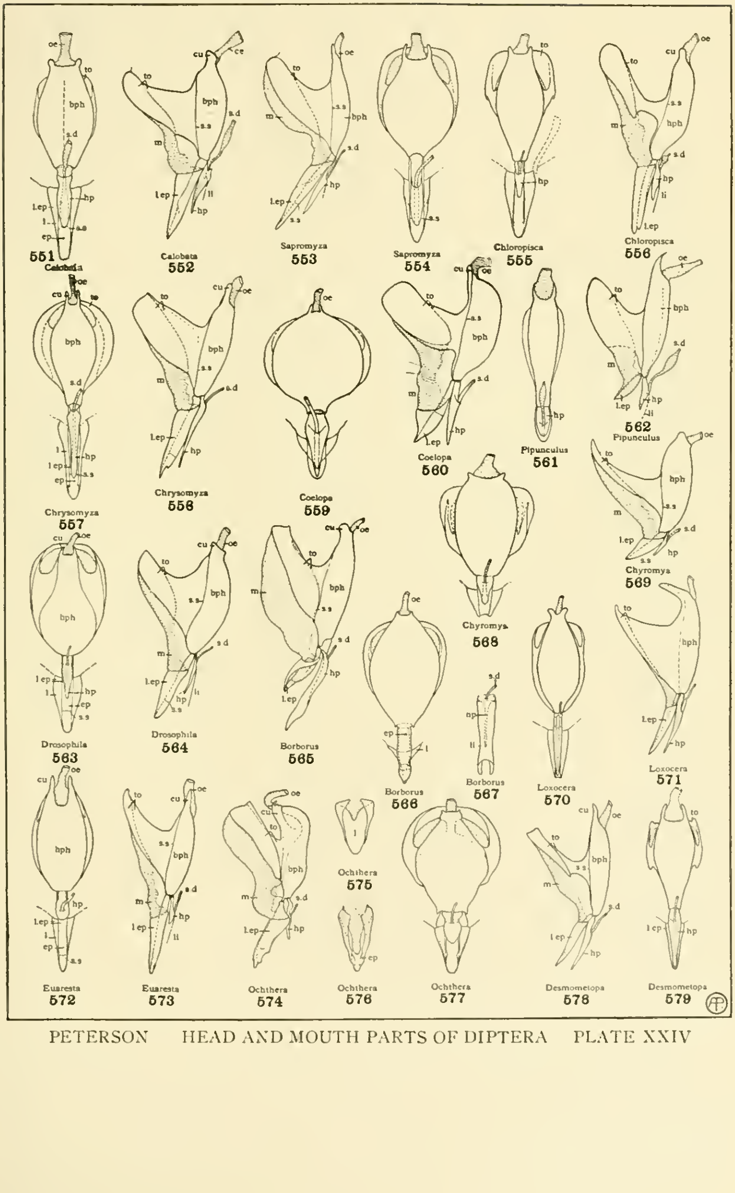
PETERSON HEAD AND MOUTH PARTS OF DIPTERA PLATE XXIII

PLATE XXIV

EXPLANATION OF PLATE

Epipharynx and Hypopharynx and Associated Parts

Fig. 551. *Calobata univitta,* caudal aspect.
Fig. 552. *Calobata univitta,* lateral aspect.
Fig. 553. *Sapromyza vulgaris,* lateral aspect.
Fig. 554. *Sapromyza vulgaris,* caudal aspect.
Fig. 555. *Chloropisca glabra,* caudal aspect.
Fig. 556. *Chloropisca glabra,* lateral aspect.
Fig. 557. *Chrysomyza demandata,* caudal aspect.
Fig. 558. *Chrysomyza demandata,* lateral aspect.
Fig. 559. *Coelopa vanduzeii,* caudal aspect.
Fig. 560. *Coelopa vanduzeii,* lateral aspect.
Fig. 561. *Pipunculus cingulatus,* caudal aspect.
Fig. 562. *Pipunculus cingulatus,* lateral aspect.
Fig. 563. *Drosophila ampelophila,* caudal aspect.
Fig. 564. *Drosophila ampelophila,* lateral aspect.
Fig. 565. *Borborus equinus,* lateral aspect.
Fig. 566. *Borborus equinus,* caudal aspect.
Fig. 567. *Borborus equinus,* hypopharynx united with labium, caudal aspect.
Fig. 568. *Chyromya concolor,* caudal aspect.
Fig. 569. *Chyromya concolor,* lateral aspect.
Fig. 570. *Loxocera pectoralis,* caudal aspect.
Fig. 571. *Loxocera pectoralis,* lateral aspect.
Fig. 572. *Euaresta aequalis,* caudal aspect.
Fig. 573. *Euaresta aequalis,* lateral aspect.
Fig. 574. *Ochthera mantis,* lateral aspect.
Fig. 575. *Ochthera mantis,* caudal aspect of the labrum.
Fig. 576. *Ochthera mantis,* caudal aspect of the epipharynx.
Fig. 577. *Ochthera mantis,* caudal aspect.
Fig. 578. *Desmometopa latipes,* lateral aspect.
Fig. 579. *Desmometopa latipes,* caudal aspect.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562 Pipunculus
563 Drosophila
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569 Chyromya
570 Loxocera
571 Loxocera
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573 Euaresta
574 Ochthera
575 Ochthera
576 Ochthera
577 Ochthera
578 Desmometopa
579 Desmometopa

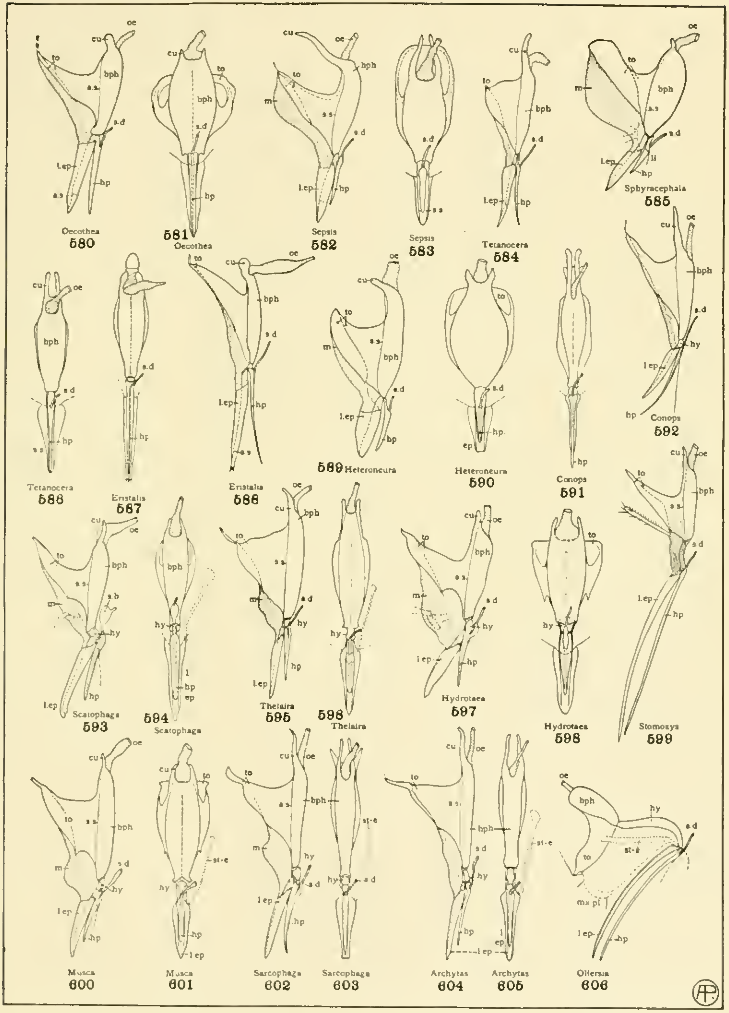
PETERSON HEAD AND MOUTH PARTS OF DIPTERA PLATE XXIV

PLATE XXV

EXPLANATION OF PLATE

Epipharynx and Hypopharynx and Associated Parts

Fig. 580. *Oecothea fenestralis,* lateral aspect.
Fig. 581. *Oecothea fenestralis,* caudal aspect.
Fig. 582. *Sepsis violacea,* lateral aspect.
Fig. 583. *Sepsis violacea,* caudal aspect.
Fig. 584. *Tetanocera plumosa,* lateral aspect.
Fig. 585. *Sphyracephala brevicornis,* lateral aspect.
Fig. 586. *Tetanocera plumosa,* caudal aspect.
Fig. 587. *Eristalis tenax,* caudal aspect.
Fig. 588. *Eristalis tenax,* lateral aspect.
Fig. 589. *Heteroneura flaviseta,* lateral aspect.
Fig. 590. *Heteroneura flaviseta,* caudal aspect.
Fig. 591. *Conops brachyrhynchus,* caudal aspect.
Fig. 592. *Conops brachyrhynchus,* lateral aspect.
Fig. 593. *Scatophaga furcata,* lateral aspect.
Fig. 594. *Scatophaga furcata,* caudal aspect.
Fig. 595. *Thelaira leucozona,* lateral aspect.
Fig. 596. *Thelaira leucozona,* caudal aspect.
Fig. 597. *Hydrotaea dentipes,* lateral aspect.
Fig. 598. *Hydrotaea dentipes,* caudal aspect.
Fig. 599. *Stomoxys calcitrans,* lateral aspect.
✓Fig. 600. *Musca domestica,* lateral aspect.
Fig. 601. *Musca domestica,* caudal aspect.
Fig. 602. *Sarcophaga haemorrhoidalis,* lateral aspect.
Fig. 603. *Sarcophaga haemorrhoidalis,* caudal aspect.
Fig. 604. *Archytas analis,* lateral aspect.
Fig. 605. *Archytas analis,* caudal aspect.
Fig. 606. *Olfersia ardeae,* lateral aspect.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Olfersia
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PETERSON HEAD AND MOUTH PARTS OF DIPTERA PLATE XXV

ILLINOIS BIOLOGICAL MONOGRAPHS

Vol. III January, 1917 No. 3

EDITORIAL COMMITTEE

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STUDIES ON NORTH AMERICAN POLYSTOMIDAE, ASPIDOGASTRIDAE, AND PARAMPHISTOMIDAE

WITH ELEVEN PLATES

BY

HORACE WESLEY STUNKARD

Contributions from the
Zoological Laboratory of the University of Illinois under
the direction of Henry B. Ward, No. 84

THESIS

Submitted in Partial Fulfillment of the Requirements for the
Degree of Doctor of Philosophy in Zoology
in the Graduate School of the
University of Illinois
1916

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INTRODUCTION

The knowledge of the trematodes of North America is very scanty. Information at hand consists largely of brief and scattered papers and comprehensive studies on the morphology of the larger groups are wanting. Such studies are needed as contributions to the knowledge of adult forms, and it is apparent also that knowledge of the anatomy and taxonomy of the adult is demanded in the solution of life history problems.

This paper contains the results of a study on the structure and classification of North American representatives of the families Polystomidae, Aspidogastridae, and Paramphistomidae. Because of certain structural and developmental features these three families are of particular interest and importance not only in the taxonomy but also in the phylogeny of the trematodes. The Polystomidae differ from all other known Heterocotylea in that they are endoparasitic; the Aspidogastridae are both ectoparasitic and endoparasitic, develop both directly and by means of an intermediate host, and in the adult condition are parasites of both vertebrates and molluscs; while the Paramphistomidae are the only forms retaining a primitive posterior sucker. These facts are significant and it is probable that further study into the structure and life history of these forms will throw considerable light on the general problems of development and taxonomy of the trematodes.

During the past three years the writer has made parasitological examinations of over three hundred North American fresh-water turtles. These comprise sixteen species collected from widely scattered localities. For assistance in securing this material, grateful acknowledgments are due Dr. N. A. Cobb of Washington, D. C., Professor A. W. Orcutt of Denison University, Professor W. E. Burge of the University of Illinois, Professor J. E. Ackert of Kansas State Agricultural College, and Professor W. W. Cort of Macalester College. The material of *Alassostoma parvum* was collected and turned over to me by Mr. T. B. Magath. A type specimen of *Polystoma coronatum* Leidy from the U. S. National Museum was placed at my disposal for study. The work was begun at the suggestion of Professor Henry B. Ward and carried on under his direction. Part of the material used in the investigation came from his private collection, and for this material as well as for criticisms and suggestions in the course of the work the writer wishes to express his appreciation.

All the forms described in this paper were studied as toto mounts; where sufficient material was available sections were made, and many were studied alive. The importance of the study of the living specimens can not be overemphasized as the best method of tracing the excretory system. Also, by observing the living animal as it moves, it is possible to measure the extent of normal variation in form that occurs in a single specimen as different shapes are assumed concomitant with the movements of the animal; in forms with such soft bodies and variable shapes, a study of preserved material alone has in many cases given false conceptions concerning morphological relationships of organs and systems. In toto mounts a support under the coverglass is necessary to prevent it from flattening and distorting the normal shape of the aspidogastrids and to avoid crushing the caudal disc of the polystomes. For the staining of specimens to be mounted in toto, better results were obtained by the use of carmine than by hematoxylin stains. For staining sections the method that proved most valuable was to use the hematoxylin stains for differentiating the nuclear elements and various plasma stains for counterstaining.

POLYSTOMIDAE

HISTORICAL REVIEW OF THE FAMILY

In 1758 Roesel von Rosenhof described and figured a "leech" from the urinary bladder of the frog. This is regarded as identical with the well known European parasite of the urinary bladder of the frog, described by Fröhlich (1791) as *Linguatula integerrimum.* M. Braun (1792) described *Planaria uncinulata* from the urinary bladder of the green water-frog and his description is so specific that there can be no doubt that he had the same form described by Fröhlich the previous year. Zeder (1800) founded the genus Polystoma to contain the three species, *Linguatula integerrimum* Fröhlich which he rechristened *Polystoma ranae, P. serratum,* and *P. pinguicola.* According to Stiles and Hassall (1908) the type was clearly intended to be *P. ranae* = *Planaria uncinulata,* and altho Braun had described the form correctly with the suckers and hooks at the posterior end of the body, Zeder erroneously stated in his characterization of the genus that the suckers were at the anterior end. *P. serratum* had been designated by Fröhlich (1789) as type of the genus Linguatula and *P. pinguicola* had been designated by Treutler (1793) as type of the genus Hexathyridium. That Zeder was in error in including these species in the genus Polystoma was demonstrated by later studies. However Rudolphi (1809) retained them in the genus Polystoma and listed three other species: *P. taenoides* Rud., *P. denticulatum,* Rud., and *P. venarum* (Treutler 1793) Zeder 1803. Among these species, it is probable that Treutler's description was of an artifact rather than a parasite, and the other two have been removed to the Linguatulidae.

Polystoma thynii was described from the gills of *Scomber thynnus* by Delaroche (1811). Rudolphi (1819) renamed this species *P. duplicatum* and added a new species *P. ocellatum* from the throat of *Emys europa.* This species is regarded as identical with that described by Kuhl and Hassalt (1822) from the nasal cavity of *Halichelys atra. P. logiginis* was described by delle Chiaje (1823) from *Loligo vulgaris.* Blainville (1828) oriented the polystomes correctly and transferred *P. integerrimum, P. ocellatum,* and *P. thynii* to a new genus Hexacotyle, naming *H. thynii* as type. According to the rules of zoological nomenclature, however, the genus Polystoma must be retained. Kuhn (1829) described *P. appendiculatum* from *Squalus catulus.* Dujardin (1845) transferred *Diclibothrium crassicaudatum* Leuck. 1835 = *Diplobothrium armatum* Leuck. 1842 to the genus Polystoma, and listed as additional species, *P. duplicatum, P. pinguicola, P. ocellatum, P. integerrimum,* and *P. appendiculatum.* Diesing (1850) named *P. loliginis* and *P. appendiculatum* as types of new genera Solenocotyle and Onchocotyle. He removed *P. armatum* to the genus Diclibothrium Leuck. and retained in the genus Polystoma only the species *P. integerrimum* and *P. ocellatum.*

The genus Polystoma together with the genera Tetrastomum, Gryporhynchus, Hexathyridium, Notocotyle, Aspidocotyle, and Aspidogaster were included by the same author in the tribe Polycotylea.

In his revision Diesing (1859) reduced the trematodes to the rank of a tribe and divided the group into three subtribes: Acotylea, Cotylophora, and Plectanophora. The second of these subtribes he subdivided into three families: Monocotylea, Tricotylea, and Polycotylea. The last of these corresponds almost identically with his former tribe Polycotylea. He rejected Gryporhynchus, and added the genera Ancyrocephalus, Plagiopeltis, Heptastomum, Onchocotyle, Cyclocotyle, and Solenocotyle. In the family Polycotylea he recognized two subfamilies: Aplacocotylea with the suckers set directly in the body, and Placocotylea with the suckers set in a median posterior plate. In the latter he included the genera Onchocotyle, Polystoma, Cyclocotyle, Aspidocotyle, Aspidogaster, and Solenocotyle.

Then followed the great work of van Beneden (1858) with an experimental demonstration of the "direct" development of the many-suckered ectoparasitic trematodes, and the "indirect" development of the distomes. For these two groups he proposed the names Monogenea and Digenea. In the former he recognized two families: the Tristomidae with a single posterior sucker, and the Polystomidae with several posterior suckers. In the Polystomidae he included the genera Polystoma, Diplozoon, Octobothrium, Axine, Onchocotyle, Calceostoma, and Gyrodactylus.

Later van Beneden and Hesse (1863) made the genera Octocotyle (= Octobothrium), Udonella, and Gyrodactylus types of new families, thus increasing the number of families to five. Many additional genera, both old and recently described, were now for the first time placed with the Monogenea. But in the family Polystomidae these authors retained only two genera, Polystoma and Erpocotyle; and in the genus Polystoma was listed only a single species, *P. integerrimum.*

Taschenberg (1879) reverted to the earlier classification of van Beneden and adopted the division of the monogenetic trematodes into two groups Tristomeae and Polystomeae, which he regarded as families Under the Polystomeae as subfamilies he listed Polystomidae, Octobothridae (= Octocotylidae), Gyrodactylidae, and the new subfamily Microcotylidae; the latter including Microcotyle, Axine, Gastrocotyle and the entirely unlike genera, Aspidogaster, Cotylaspis and Aspidocotyle. To the Polystomidae he added the genera Onchocotyle and Diplobothrium, and in the genus Polystoma included the two species *P. integerrimum* and *P. ocellatum.*

In regard to the previously mentioned forms St. Remy (1891) followed the family and subfamily divisions of Taschenberg, tho adding new genera to each of the subfamilies and removing Aspidogaster, Cotylaspis, and Aspidocotyle from the Microcotylidae. To the Polystomidae, Wright and Macallum had added the genus Sphyranura, and in the genus Polystoma were listed the new species *P. oblongum* Wright and *P. coronatum* Leidy.

Increased knowledge of the trematodes disclosed so many exceptions to their classification according to life history that Monticelli (1892) proposed a new arrangement of the group, based on morphological characters. To contain the forms previously classed as Monogenea, he proposed the suborder Heterocotylea. He raised the Monocotylidae and Gyrodactylidae from subfamily to family rank, making five families in the Heterocotylea. In the family Polystomidae he retained the subfamilies Polystominae, Octocotylinae, and Microcotylinae of former authors.

So far as the Polystomidae are concerned, the synopsis of Pratt (1900) does not differ from that of St. Remy and Monticelli.

Later Monticelli (1903) worked out a new classification of the Heterocotylea, separating the forms on the basis of differences in the adhesive apparatus. He arranged the families in two tribes, Oligocotylea and Polycotylea, the former containing the forms with few suckers and the latter those with many suckers. This division he says is not of great systematic importance but may be of practical value in the identification of families. In the Oligocotylea he included the families Tristomidae, Monocotylidae, Udonellidae, Calceostomidae, Gyrodactylidae, and Dicotylidae; and in the Polycotylea the families Polystomidae, Octocotylidae, Hexacotylidae, Platycotylidae, Pleurocotylidae, and Microcotylidae. Among these the Udonellidae, Octocotylidae, and Microcotylidae are raised from subfamily to family rank, and the Calceostomidae, Dicotylidae, Hexacotylidae, Platycotylidae, and Pleurocotylidae are new families. The family Polystomidae contained the single genus Polystoma with the species *P. integerrimum, P. ocellatum, P. oblongum, P. coronatum,* and *P. hassalli.*

Discussing the classification of Monticelli, Odhner (1912) stated that he considered the number of suckers of secondary importance and the system based on them therefore lacking in fundamental systematic significance. Accordingly he rejected the work of Monticelli, and using the older classification of Monogenea, divided the forms within the group on the basis of differences in the female reproductive ducts. He discussed the relationship of the ducts of the female genital system in various trematode and cestode genera, and stated that he was convinced as was claimed by Stieda that Laurer's canal of the trematodes should be regarded as homologous with the vagina of the cestodes. Intervening authors, Looss (1893), Goto (1894) and several other writers, had considered Laurer's canal of the Malacocotylea as homologous with the genito-intestinal canal of certain Heterocotylea, and not with the vagina of the cestodes. Odhner argued that Laurer's canal was the primitive vagina of the trematodes and that there had been a change of vaginal function from this canal to the terminal part of the uterus, with the resulting degeneration of the former duct. It now served in his opinion only to carry off excess spermatozoa, together with yolk and shell substance not used in the formation of the eggs. He adds that there is no evidence on which to base an explanation of the transfer of the seat of vaginal function from Laurer's canal to the terminal part of the uterus; it must only be accepted as a fact.

According to Odhner, in the group of monogenetic trematodes, two very different structures are included under the term vagina. One present in the Tristomidae, Monocotylidae, and Gyrodactylidae opens to the exterior on the left side of the ventral surface, and at the inner end is enlarged to form the seminal receptacle. This tube he considered homologous to the vagina of the cestodes and Laurer's canal of the digenetic trematodes. The other structures which he did not consider homologous to this true vagina were the ducts of the Octocotylidae, Polystomidae, and Microcotylidae, which function as vaginae and open into the vitelline collecting ducts. These are paired and open to the surface either ventrally, laterally, or dorsally. Contending that they had arisen *sui generis*, he proposed for them the name "ductus vaginalis." Considering the question of whether the paired or unpaired condition of these ducts was primitive, he argued that originally the duct was unpaired and opened ventrally; that the opening became divided and the duct split, therefore the Y-shaped duct of Rajonchocotyle must be considered as a stage in the development of the paired condition of the ducts. A further separation would give the lateral openings of Polystoma. In the Microcotylidae the openings have migrated dorsally and fused producing a single dorsal tube. Odhner could find no homologue for the genito-intestinal canal and since he maintained that it was not homologous with Laurer's canal, concluded that it had arisen *sui generis.*

On the basis of these differences in the female genital ducts he divided the Monogenea into two suborders: Monopisthocotylea and Polyopisthocotylea. The former is characterized by the absence of the genito-intestinal canal, the presence of a "true vagina" and a single posterior organ of attachment; the latter by the presence of the genito-intestinal canal, "ductus vaginalis," many posterior adhesive organs, and the absence of a "true vagina." In the Monopisthocotylea he included the families Tristomidae, Monocotylidae, Udonellidae and Gyrodactylidae; and in the Polyopisthocotylea the families Polystomidae, Microcotylidae and Octocotylidae. He pointed out that by the removal of the genus Sphyranura, the Oligocotylea, the first of Monticelli's tribes agrees entirely with his suborder Monopisthocotylea. In the second of Monticelli's tribes, however, the Diclidophorinae, together with the genera Dactylocotyle and Hexacotyle, should be removed from the Octocotylidae and placed with the Microcotylidae, since they more nearly agree with the latter forms in internal structure.

The next year Odhner (1913) reaffirmed his idea of the homology of the vagina of the cestodes and Laurer's canal of the distomes, but explained therewith that his denial of the homology of the genito-intestinal canal and Laurer's canal had been based on an error of Cerfontaine in describing an unpaired vagina as present in the genus Dactylocotyle. On examination of this genus he had found that a "true vagina" was absent, and concluded that the "true vagina" of the Monopisthocotylea which he had homologized with Laurer's canal was never present together with the genito-intestinal canal. From this he decided that the "true vagina" was homologous with the genito-intestinal canal and therefore with Laurer's canal. Now maintaining the homology of the "true vagina" and the genito-intestinal canal he is in my opinion obliged to dismiss the presence or absence of the genito-intestinal canal as a basis of difference between his suborders, and explain why in one group this canal opens to the exterior on the ventral side of the body and in the other opens into the intestine. His homology of the "true vagina" and the genito-intestinal canal is a most serious error since it would invalidate the distinguishing feature which separates the two suborders.

I propose to show that the organ which functions as a vagina is homologous in all the monogenetic trematodes, and that there can be no division of the group on the basis of differences suggested by Odhner. In fact, the work of Odhner is based on an incorrect assumption and false homologies. Starting with the assumption that Laurer's canal is homologous to the vagina of the cestodes, he has missed the truth in his entire discussion and when at a loss to explain a structure has derived it *sui generis*. His later paper (1913) admitting the homology of Laurer's and the genito-intestinal canals corrected one mistaken contention, but his separation of the female copulatory ducts into a true vagina and "canalis vaginalis" seems entirely without foundation. There is no evidence to support the idea that the single vagina is not homologous to the paired vaginae. In fact, Odhner described the paired vaginae as arising by the division of a single unpaired tube, probably ventral in position. He derived this tube *sui generis*, and cited no reason why it is not homologous with the ventral unpaired vagina of the Monopisthocotylea. Further he gives no means of distinguishing between the two.

Looss (1893) presented a strong argument to prove that Laurer's canal is not a vagina, nor homologous to the vagina of the cestodes.

Goto (1894) reveiewed the literature up to that date and gave a careful and detailed study of the *canalis genito-intestinalis*. Making a very clear and comprehensive analysis of the question and summarizing evidence from a wide study of ectoparasitic forms, he concluded that the genito-intestinal canal and Laurer's canal are homologous and that neither are homologous with the vagina of the Monogenea. He showed that in the group there is a perfect series of vaginae from a truly paired to a truly unpaired condition. He discussed the idea of Braun who regarded the presence of a single vagina as the result of a simple atrophy of one of the originally paired vagina, with the conclusion that the relations of the ducts "point strongly to the view that the unpaired vagina has been formed by the union and subsequent displacement of the originally paired vaginae, and not as Braun supposes by the atrophy of one of them."

In the present study, the histological character and the relative position and relationships of the ducts of the female system support the contention of Looss and Goto that Laurer's canal is homologous with the genito-intestinal canal, and affords no evidence that these ducts have any further homologue. A review of the literature and the study of the ducts in the three families discussed in this paper has convinced me that Laurer's canal is homologous to the genito-intestinal canal;and the vagina of the Monopisthocotylea is homologous with the originally single, subsequently paired, and secondarily fused vaginae of the Polyopisthocotylea. It makes no difference whether the single or paired condition is regarded as primitive. Given a single unpaired vagina as described by Odhner for the Monopisthocotylea; by a division of the external part and subsequent lateral migration of the openings, the paired vaginae of the Polyopisthocotylea are explained. These ducts entering the body from the sides, lying parallel with the vitelline ducts and discharging into the same cavity, became fused at their internal ends with the vitelline ducts and this union continued outward to the location where the vitelline ducts turn toward the follicles and the vaginae branch off to open to the exterior. The advantage of a single duct over two ducts lying side by side is obvious, and the fusion of two parallel ducts is not uncommon in other groups. With a further dorsal migration of the opening of the vaginae there would be a separation of the vitelline and vaginal canals and a dorsal fusion of the vaginae would give the single dorsal vagina of Octobothrium, Axine, and Microcotyle. The earlier fusion of the vitelline and vaginal canals would retard the secondary fusion of the internal ends of the dorsal vaginae and this explains the single dorsal pore and internally paired vagina of *Axine heterocerca* which is used by Odhner as an argument supporting his idea that in the Monogenea two different structures are included under the term vagina.

I agree with Odhner that the seminal receptacles of Sphyranura are homologous to the paired vaginae of Polystoma, and that this furnishes a splendid example of the change whereby the terminal part of the uterus has assumed the copulatory function. It may be that further specialization in this direction, due to the endoparasitic habit and self fertilization, may explain the absence of the vagina of the distomes.

It now remains only to account for the absence of the genito-intestinal canal in the Monopisthocotylea. Odhner stated that this structure is homologous with Laurer's canal, and in his (1912) paper called attention to the fact that Laurer's canal is a "rudimentary organ" which serves no essential function. The vestigeal character of Laurer's canal is believed in by most writers—Looss, Monticelli, Brandes, Goto, etc. This structure is entirely lacking in some distome groups and in others is represented by a blind sac opening from the ootype. Since the genito-intestinal canal is admittedly homologous to Laurer's canal and the latter is known to be a vestigeal structure, it appears reasonable to suppose that it has degenerated in the Monopisthocotylea.

There is a possibility that the Monopisthocotylea instead of having lost a genito-intestinal canal may have arisen from a group of the Turbellaria which had no homologous structure, but this explanation seems very improbable. Haswell (1907) described in certain Australian polyclads a tube which formerly had been considered an accessory or dorsal vagina but which in certain forms opened into the intestine. The presence of this genito-intestinal canal in polyclads, he says, "strengthens the contention, so ably supported by Goto, that the genito-intestinal canal and not the vagina of the Heterocotylea is the equivalent of the Laurer's canal of the Malacocotylea."

The absence of the genito-intestinal canal in the Monopisthocotylea is undoubtedly a feature of distinct taxonomic importance, and the work of Odhner is an advance step in the formation of a natural system and the final classification of the monogenetic forms. Since the arrangement of Monticelli, based on the character of the adhesive apparatus, so nearly agrees with that of Odhner which in reality is based on the presence or absence of a genito-intestinal canal, it appears that both these features are of large importance in the taxonomy of the group. Present evidence is insufficient to decide which is of greater significance. Further study may show that there is complete agreement in classifications based on both features.

Odhner (1912) argued that the removal by Monticelli of Sphyranura from the family Polystomidae on the basis of the difference in number of suckers was not justified. As previously stated, the writer agrees with Odhner that the seminal receptacles of Sphyranura are homologous with the vaginae of Polystoma, and the agreement in type of genital ducts indicates a closer relationship between these genera than is assigned in the system of Monticelli. Sphyranura undoubtedly should be placed with the Polyopisthocotylea. There are, however, wide and fundamental differences between it and the genus Polystoma, and while future researches may discover intermediate forms which will make it possible to include them with certainty in a single family, for the present such a grouping is hardly justified and the two families should be retained, altho the name Dicotylidae of Monticelli does not conform to the rules of zoological nomenclature.

THE GENUS POLYSTOMA

The family Polystomidae as considered in this paper contains only the genus Polystoma. The members of this genus are widely distributed, species having been described from all the continents except South America. The species are not only widely distributed geographically, but also vary widely in type of host and in location within the host. They are parasitic in the urinary bladder of frogs and toads and on the gills of frog larvae, and also infest the urinary bladder and pharyngeal cavity of many species of turtles.

The structure and development of *Polystoma integerrimum* has been investigated by Stieda (1870), Zeller (1872 and 1876), Willemoes-Suhm (1872), Halkin (1902), Goldschmidt (1902), and André (1910). Zeller (1876) described two forms of *P. integerrimum,* one which became mature in the urinary bladder of the frog, and the other which became mature on the gills of the frog tadpole. These two forms of the parasite show wide differences in size and internal structure. The form which becomes mature in the urinary bladder is much larger, has a lobed testis, external vaginae, and a long coiled uterus which contains many eggs. The form maturing on the gills of the tadpole has a spherical testis, lacks external vaginae and a long coiled uterus, and has a small uterine cavity in which a single egg develops. Halkin and Goldschmidt have investigated the early stages in this form, but the writer has been unable to find any reference to work on the later larval stages. The findings of Zeller are so unusual that one is led strongly to suspect he confused two different species.

The descriptions of *P. ocellatum* by Rudolphi (1819) and Kuhl and Hassalt (1822) are very brief; that by Willemoes-Suhm (1872) contains one plate, and Looss (1885) figured only the structures at the distal ends of the excretory tubules.

The description of *P. oblongum* Wright (1879) contains sufficiently detailed information for a specific diagnosis and is illustrated by three figures. Stafford (1905) reported *P. oblongum* from the palate of *Chrysemys picta* and the same location in *Chelydra serpentina,* but since Wright originally described the species from the urinary bladder of *Aromochelys odoratus,* Braun reviewing Stafford's article considered the form from the oral cavity as a different species. The form described by Leidy as *P. oblongum,* was reinvestigated by Goto (1899) and proved to be a different species from that described by Wright, but the material he reports was in such a poor state of preservation that renewed study was impossible and so the form must remain unknown.

Leidy's (1888) description of *P. coronatum* is so brief that it is almost valueless; a type specimen mounted as a toto preparation has been available for the present study and many additional points of structure are added to the original description.

P. hassalli was described by Goto (1899) from the urinary bladder of *Cinosternum pennsylvanicum* and has been collected by the writer from the urinary bladder of *Aromochelys odoratus, A. carinatus,* and *Chelydra serpentina,* as well as from *Cinosternum pennsylvanicum.* Additional data correct and supplement the description of Goto.

Johnston (1912) described *P. bulliense* from the urinary bladder of two species of Hyla from New South Wales, Australia. Beauchamp (1913) described *P. alluaudi* from an unknown batrachian from the lower prairies of Kinangop, Africa; the material was collected by the African expedition of Alluaud and Jeannel. Stewart (1914) described *P. kachugae* from the urinary bladder of the water tortoise, *Kachuga lineata,* at Lucknow, India.

In the genus Polystoma present evidence supports the validity of the following described species listed in the order of description:

P. integerrimum Frölich 1791. From the urinary bladder of frogs and toads and the gills of frog larvae; Europe.

P. ocellatum Rudolphi 1819. From the throat and nasal cavity of *Emys europa and Halichelys atra;* Europe.

P. oblongum Wright 1879. From the urinary bladder of *Aromochelys odoratus;* North America.

P. coronatum Leidy 1888. From the fauces of the terrapin; North America.

P. hassalli Goto 1899. From the urinary bladder of *Cinosternum pennsylvanicum, Aromochelys odoratus, A. carinatus, and Chelydra serpentina;* North America.

P. bulliense Johnston 1912. From the urinary bladder of *Hyla phyllochros* and *H. Lesueurii; Australia.*

P. alluaudi, Beauchamp 1913. From an unknown batrachian; Africa.

P. kachugae Stewart 1914. From the urinary bladder of *Kachuga lineata;* India.

In the present work evidence is submitted to justify the inclusion of the following new species:

P. orbiculare Stunkard 1916. From the urinary bladder of *Pseudemys scripta* and *Chrysemys marginata;* North America.

P. opacum Stunkard 1916. From the pharynx of *Trionyx ferox* and *Malacoclemmys lesueurii;* North America.

P. megacotyle Stunkard 1916. From the mouth of *Chrysemys marginata;* North America.

P. microcotyle Stunkard 1916. From the mouth of *Chrysemys marginata;* North America.

With the exception of *P. integerrimum,* the members of the genus are very rarely found and the number of individuals discovered is very small. Wright described *P. oblongum* from two specimens; Leidy, *P. coronatum* from four specimens; Johnston had sixteen specimens of *P. bulliense;* Beauchamp described *P. alluaudi* from a single specimen; Stewart had only two specimens of *P. kachugae.* The writer had only a limited number of individuals of any species; *P. microcotyle* was described from a single specimen; *P. orbiculare* from nine specimens; *P. opacum* and *P. megacotyle* each from three specimens. Because of the limited amount of material, it has been impossible to attempt special technique to differentiate the various organ systems, and the descriptions are therefore incomplete in certain particulars. The general morphological features are however described in sufficient detail that clear specific diagnoses can be made, and in certain instances the finer structure and histology of the organs has been described.

ANATOMY AND HISTOLOGY OF THE POLYSTOMIDAE

The species that have been included in the genus Polystoma show a much wider range of structural variation than is usually present in a natural genus. There are wide differences in the character of digestive and reproductive systems, and variation exists in the type of adhesive apparatus.

There is wide variation in size; *P. integerrimum*, the largest known species measures up to 12 mm. in length, and *P. hassalli* is only 1.3 to 2 mm. in length. The width is one-third to one-fifth of the total length. All the worms that have been included in this genus have a flattened, elongate oval body which at the posterior end bears a large ventral muscular disc or cotylophore. The body is more or less pointed at the anterior end and at the posterior end may or may not have a constriction just before the attachment of the caudal disc. As in all trematodes the shape is subject to considerable variation as the animal elongates and contracts. Locomotion is accomplished by attaching the anterior sucker and then bringing the caudal disc forward; as a result of the terminal attachments and the "looping" method of progression, the dorsal line of the body is more or less arched and the ventral surface is concave. In certain species at the openings of the vaginae on the lateral or ventrolateral margins of the body, there are prominent swellings, the "Seitenwülste" of Zeller. These structures are not present in any of the known North American species.

Organs of Attachment.—The caudal disc bears on its ventral face the chief organs of attachment. These consist of suckers and hooks, the former arranged in pairs, three suckers on each side of the median line. The two posterior suckers are close together and those of the middle pair are separated by a considerable distance, while the anterior pair may or may not be near each other. In all previously reported forms except *P. alluaudi*, the anterior suckers are separated by a considerable distance, giving the disc the shape described by Leidy as cordiform (Fig. 27). In the single specimen of *P. alluaudi* described by Beauchamp, both the caudual and cephalic suckers are separated, while those of each side are contiguous. In *P. orbiculare* the anterior suckers are in the same close proximity as the caudal pair, and each sucker of the disc is separated from the two adjacent to it by uniform distances, making a perfect circle of suckers (Fig. 1). In the six species described by the writer these suckers are complicated structures, set more or less deeply in the parenchyma of the caudal disc. Their structure, character of insertion, muscular attachments, and relation to the surrounding tissue indicate that they are protrusible and retractile, and in fact such movements may be observed by watching the live worm.

The suckers are cup shaped (Fig. 34), and in all the species described in this paper are constructed on an elaborate cuticular framework. According to Zeller the sucker forms as a ridge around a larval hooklet and later sinks into the parenchyma, and this method of origin explains the cuticular covering of the external and internal surfaces of the cup. Running across between these cuticular membranes, there are short refractive fibers which constitute the mass of the wall of the sucker (Fig. 35). Wright and Macallum (1887) describing similar fibers in the walls of the suckers of Sphyranura say, "Instead of the substance of the sucker being formed of muscular fibers disposed in three directions, and capable of modifying the shape of the cavity, as in the distomes, it is not possessed of contractility in Sphyranura (and probably in Polystoma), and is formed of prismatic fibers, rather of a supportive than a muscular character, arranged perpendicularly between the concave and convex limiting membranes of the suckers." Goto (1894) described similar fibers in the suckers of Axine, Microcotyle, Octocotyle, Diclidophora, Hexacotyle, and Onchocotyle and considered them to be more of an elastic than a contractile nature. They are, he states, different from the ordinary muscular fibers of the body and from those of the suckers of the Tristomidae and Monocotylidae, as well as from those of the anterior sucker of Onchocotyle, both in optical characters and in reaction toward staining fluids. The structure of the suckers in these forms and their mode of operation are discussed by Goto at considerable length, but as the suckers he described are constructed on a different type of cuticular framework from that present in the genus Polystoma, obviously the type of suctorial action is different.

In all the species described in this paper, the fibers which form the walls of the posterior suckers are similar to those described by Wright and Macallum and Goto; the cuticular framework is also flexible and elastic, but is of a different type from that described by Goto. In the polystomes investigated by the writer, with the exception of *P. integerrimum,* the sucker consists of three sections or zones which may be designated as basal, intermediate, and external or distal (Fig. 36). The external part or rim of the sucker is supported by numerous cuticular rods formed by the thickening at regular intervals of the cuticular lining. These rods are bent outward, their curvature maintaining the flare of the rim of the sucker. Distally they terminate just inside the rim of the cup and basally they are continuous with and are processes from a band of cuticula which passes around the sucker and separates the external and intermediate portions. In toto preparations this band appears to be divided into sections that are almost square, each with a circular area in the center that increases and decreases in size as the focus is changed.

Sections show that the cuticular lining of the sucker is folded outward against the convex wall with which it is fused, thus interrupting the continuity of the fibrous wall (Fig. 35). The two sides of this invaginated cuticular sac or ring are fused at regular intervals, leaving small pockets alternating with the places of fusion. These small openings in the cuticular band are conspicuous by reason of their different refractive index and show very plainly with a dark field illumination as the square or rectangular sections with the circular areas in the center (Fig. 34). There is apparently no relation between the number of these sections in the cuticular band and the number of cuticular thickenings which serve as supports of the external section.

The middle section of the sucker extends basally from the previously described cuticular band to a somewhat similar evagination of the cuticular lining into the wall of the sucker, but this evagination does not extend to the external cuticular covering of the sucker and only partially divides the fibrous wall. This middle or intermediate portion of the sucker is supported by thickenings of the cuticular lining, processes that extend peripherally from the cuticular band which passes around the sucker at its base. These supporting ridges are not arranged at regular intervals and they are much fewer in number than the cuticular rods which support the external section. They are often branched, tho not more than a single bifurcation was observed.

The basal portion of the sucker is circular, similar in structure to the portions previously described; it has internal and external limiting membranes with fibers extending between. At its center the cuticular and fibrous wall is interrupted and there is the structure described by Johnson (1912) as the connective tissue plug, which appears as a central disc or button, and to which the retractor muscles are attached. This central disc has thickened cuticular edges and bears the larval hooklet. Figure 44 illustrates the method of operation of the suckers. Muscles are attached to the external wall of the distal and intermediate portions of the sucker and the contraction of these muscles retracts the two external zones, with the accompanying protrusion of the basal part. Whether the small hooks at the bases of the suckers are functional is doubtful. As previously described, the cuticular supports do not extend quite to the external margin of the sucker, leaving a soft plastic edge which can be applied all the way around even on an irregular surface. With the contraction of the muscles attached to the basal disc, a vacuum is produced and forms a powerful means of adhesion. Since the walls of the sucker are not contractile and the suckers vary only slightly in size in a single species, the size of the suckers has been used by the writer as a character for determining specific identity.

A cuticular framework similar to that present in Polystoma was described by Wright and Macallum for the suckers of *Sphyranura osleri.* They say: "As the wall of the sucker is itself destitute of contractility, another arrangement exists for modifying the shape of the cavity. Its walls is really divided into three concentric zones, which by special extrinsic muscles can be worked independently. The two circular lines which separate these zones, are marked by an infolding of the investing membrane, which forms a sort of joint, permitting an independent movement of the zones."

The collection of Professor Ward contains a single series of sections of *P. integerrimum* from Germany, and in this specimen the type of skeletal structure just described is absent. Figure 45 shows the character of the suckers in this form. The caudal disc typically bears eighteen hooks. Sixteen are similar in size and shape, arranged as follows: six in a row between the anterior suckers, one situated inside each sucker at the base, and four between the two posterior suckers. In addition to these hooks there is a pair of great hooks, several times the size of the small hooks, between the two posterior suckers. The shape of these hooks and their arrangement are shown in Figures 37 to 43. In many cases there is only one pair of the small hooks between the caudal suckers; in such cases in addition to the great hooks there is a third pair, similar in shape to the great hooks and intermediate in size between the great and small hooks.

The sixteen small hooks are present on the caudal disc of the larva before the suckers are formed and are called larval hooklets by Willemoes-Suhm (1872), but Zeller (1876) says: "Die sechszehn kleinen Häkchen mit ihren Oesen, welche die Haftscheibe angehoren und welche bei der Polystomum larva so ausserordentlich deutlich zu erkennen ist, sind nicht, wie Willemoes-Suhm meint, nur 'Larvalorgane'. Sie werden nicht abgeworfen, sondern sind wie ich auf das bestimmeste wiederholen muss, bei der erwachsenen Thiere noch sämmtlich vorhanden, sehr beweglich und gewiss nicht ohne Bedeutung für ein festeres Anheften." Johnston (1912) in the description of *P. bulliense* says: "Four larval hooklets are present in a row on the ventral surface near the posterior edge of the disc or cotylophore. I have been able to find no trace either in the living worms or the fixed material, of the larval hooklets which *P. integerrimum* and other species bear near the anterior edge of the disc. There is a small anchor shaped hook in the base of each sucker. All these hooks either disappear as the animal increases with age, or very readily become detached. In only one out of sixteen specimens have the whole four posterior hooklets been present; and in only two others were any hooklets at all to be seen. In all other specimens no hooklets could be made out."

In my own material I find that the larval hooklets are invariably present in the bases of the suckers, but of the other larval hooklets, usually several are absent and often those present are so arranged that it is difficult to see how they could function in attachment. Those at the anterior edge of the caudal disc are seldom regularly arranged, and in many cases (Figs. 37 to 43) are in such irregular and unusual positions with reference to each other that the use of one would interfere with the action of the others.

The great hooks are invariably present in the species in which the caudal disc is cordiform in shape, i. e., where the two anterior suckers are separated by a distance exceeding that between the two posterior suckers. In the species *P. alluaudi* and *P. orbiculare* the disc is circular and the great hooks are absent. Usually the cordiform disc is wider and the circular disc is narrower than the body. At first it seemed possible to separate the genus into two subgenera, one in which the disc is circular and the great hooks are absent and another with a cordiform disc and great hooks present, but there seems to be no such clear line of separation. In *P. orbiculare* a large number of chitinous spicules are present on the disc, some between the suckers and the others in the central area of the disc. In *P. opacum* the disc is intermediate in shape; it is difficult to determine whether it is circular or cordiform, and the great hooks are present altho they are not more than half the size of those in other species (Fig. 40). In *P. hassalli* the disc at times may be circular and the great hooks are strongly developed (Fig. 31).

Body Covering.—The body is covered with a non-cellular, unarmed cuticula, which is turned in at the external openings of the various systems. It does not have a uniform appearance but is traversed by lines which extend perpendicular to the surface of the body.

Musculature.—The musculature consists of the dermo-muscular sac, the muscles of the adhesive apparatus, and dorso-ventral strands with much-branched fibers which traverse the body at irregular intervals. The muscles of the body wall consist of an external circular layer, an intermediate layer of diagonal fibers, and inside the latter, bundles of longitudinal fibers. In all the species studied, the inner longitudinal fibers are more strongly developed than either of the other layers. Stieda (1870) in *P. integerrimum* did not distinguish between the two external muscle layers and described only two layers of muscles, an outer layer of annular fibers, some of which were not exactly circular and crossed each other, and an inner layer of longitudinal fibers. Zeller (1876) was in error when he described the diagonal fibers as inside the longitudinal layer in *P. integerrimum*. The arrangement of the muscles of the body wall in Polystoma is the usual condition in the Heterocotylea, and a similar arrangement has been described in Calicotyle, Axine, Nitzschia, Tristomum, Octobothrium, Temnocephala, Microcotyle, Octocotyle, and Monocotyle. In Diclidophora Goto (1894) described an additional layer of longitudinal fibers between the circular and diagonal layers. He states that in Onchocotyle and Hexacotyle the circular fibers seem to be entirely lacking. In the genus Polystoma there are strong sets of longitudinal fibers near the median line on the ventral side of the body. They could be traced anteriad only to the testis. Posteriad they pass into the caudal disc and together with fibers from the body wall are inserted on the sides and in the bases of the bothria. Muscle strands from both sides of the body pass to each of the suckers (Fig. 29) and smaller groups of fibers from each sucker to each of the others. In addition to the dorso-ventral muscles which extend between various points of the body wall, there are other fibers from the body wall to the internal organs.

Mesenchyma.—The mesenchymal tissue of the body does not show a differentiation into ectoparenchyma and endoparenchyma as described by Brandes (1892) and other writers; it is not of a uniform character, but presents differences in appearance at different points in the same specimen. It may take the form of compact cellular tissue, or of vacuolated cells, or there may be large vacuoles apparently between cells, or the cellular structure may be entirely lacking, there being only a reticulum of fibrous tissue. The parenchyma is traversed by many muscle strands, and the dorsal and lateral regions are occupied by the enormously developed vitellaria (Figs. 19, 23).

Alimentary System.—The digestive apparatus consists of a terminal anterior or oral sucker, a pharynx, a short esophagus and a bifurcate intestine. The oral sucker (Fig. 6) is not fully homologous with that of the distomes. There is no external limiting membrane, branched muscle fibers passing from the inside lining of the sucker to the body wall. Posteriorly it is limited and separated from the body parenchyma by special strands of fibers which pass from the body wall to the wall of the digestive tube and are attached there just anterior to the pharynx. A contraction of these fibers causes the constriction between the anterior sucker and the body parenchyma which is sometimes seen. Longitudinal muscle fibers from the body parenchyma penetrate this posterior boundry of the anterior sucker and pass to the wall of the sucker. Annular muscles, situated just inside the cuticular lining, pass around the sucker from side to side. Situated among the muscle fibers there are large secretory cells. Johnston described the structure as a weakly developed or incipient oral sucker. The anterior sucker, pharynx, and esophagus are lined with cuticula continuous with that of the external surface of the body.

The pharynx is approximately spherical, altho various states of contraction influence its shape to some extent. It does not lie directly in the long axis of the body but obliquely, the lumen extending from the somewhat ventral anterior opening from the oral sucker to a more dorsal posterior opening into the esophagus or intestine. In certain species it is composed of two portions, (Figs. 6, 33) tho both are enclosed in the same external capsule. In the anterior portion there are many strong annular fibers and this part probably acts as a sphincter, altho there are also radial fibers which extend from the external limiting membrane to the cuticula of the lumen. In the posterior part the annular fibers are confined almost entirely to the external region and a small central zone (Fig. 25). The muscle fibers are branched and non-nucleated. Scattered among the fibers in the posterior part there are large nuclei, each with a deeply staining nucleolus and surrounded by a granular or flaky area that is continued by a fine duct traceable by the presence of the same granular substance and leading to the lumen of the pharynx. Goto described somewhat similar nuclei in the pharynx of Diclidophora and regards them as remnants of the cells that have produced the muscle fibers. The writer is inclined to the view that in Polystoma the granular substance is a secretion. No extra-esophageal glands were observed, but that the secretion of the pharyngeal cells is salivary was not demonstrated.

A short esophagus may be present in certain species (Fig. 6) but in most cases the pharynx appears to open directly into the intestine at the juncture of the right and left ceca. There may be a short median or paired lateral pockets of the intestine extending anteriad from the junction of the ceca.

There is wide variation in the type of the intestinal diverticula. In *P. integerrimum* the ceca are much branched and these branches ramify thru the body and the caudal disc (Fig. 45). In *P. alluaudi* the ceca occupy the same location but are merely lobed and have no secondary branches, tho they are united posteriorly. In *P. bulliense,* according to Johnston, "a diverticulum from the buccal cavity runs backwards, ventral to the pharynx, and for a distance equal to its length forming a median unpaired buccal pocket." In all other known species there is a simple bifurcate intestine, the ceca terminating just anterior to the caudal disc. In two specimens of *P. hassalli,* however, the ceca are connected posteriorly; in one of them the ends of the ceca are continuous and in the other there is a connection some distance anterior to the ends of the ceca (Fig. 30). The walls of the diverticula are composed of a delicate fibro-membranous tissue upon which rests the digestive epithelium. The epithelial layer consists of columnar cells whose nuclei lie near the fibro-membranous sheet and which have large, rounded, often vacuolated bodies extending irregularly into the canal. The protoplasm of the cells is granular.

Excretory System.—In this family as in all Heterocotylea, there are two excretory pores, situated on the dorsal surface about midway between the median line of the body and the lateral edge of the worm, near the level of the caudal margin of the pharynx (Fig. 27, 33). These open from vesicular expansions, which when filled are almost spherical and when empty have folded walls. The descending collecting duct originates in the region of the pharynx from the fusion of smaller ducts and passes posteriad to the region of the caudal disc where it turns cephalad and continues as the ascending collecting duct to open into the excretory vesicle. Both the descending and ascending ducts receive smaller branches at irregular intervals; at the caudal end of the body a canal joins the tubes of the two sides and a similar connection exists between the descending ducts just anterior to the pharynx. From this anterior communicating canal a branch enters the anterior sucker near the median line. The excretory vesicles are lined with a thin layer of cuticula continuous with that of the external surface of the body and the collecting ducts and accessory branches have a fibro-membranous wall in which nuclei are occasionally embedded. In *P. integerrimum*, Zeller described many connections of the collecting ducts of the two sides thru anastomoes of their smaller branches. He also described cilia on the walls of the collecting ducts. Looss (1885) described the excretory system of *P. ocellatum.* He says the collecting ducts are not ciliated throuout, but only in occasional areas, and describes cilia in the capillaries. These capillaries are long and at the distal end are very much coiled. In this coiled part the capillary is divided so that two flame cells discharge into each coil and are emptied by a single capillary. The caliber of the excretory vessels is very minute, and altho varying somewhat as a result of distention, lacunar expansions were not observed. Because of the limited amount of material, much of which was received in a preserved condition, no attempt was made to trace the excretory system in living worms of this family. The vitellaria completely obscure the excretory ducts in toto preparations. The secondary ducts are so small and so often collapsed that it is impossible to follow their continuity with certainty in sections.

Nervous System.—The morphology of the nervous system of *P. integerrimum* was described in detail by André (1910). He described a supra-esophageal brain from which three pairs of nerves pass anteriad and three pairs posteriad. In another paper (1910a) he gave a detailed description of the eyes of *P. integerrimum.* In the present work no special study of the nervous system was made and no new facts were adduced.

Male Reproductive System.—The testis is a much branched structure in *P. kachugae;* in *P. integerrimum* it is lobed, and in the other known species it is oval or spherical. It is situated near or slightly anterior to the middle of the body. A duct designated an internal vas deferens was described in *P. integerrimum* by Zeller, but Ijima (1884) traced the true relations of this tube and showed that it passes from the ootype to the intestine. Goto (1894) proposed the name *canalis genito-intestinalis* for this structure which is discussed in a later section. The vas deferens arises from the dorso-cephalic margin of the testis and passes dorsad and anteriad. It extends dorsal to the ootype, between the dorsal margins of the ovary and uterus to the level of the genital pore where it turns ventrad and enlarges to form the seminal vesicle (Fig. 13). From the seminal vesicle a duct passes thru the cirrus sac, opening into the genital atrium (Fig. 26). The vas deferens is small and has a fibro-membranous wall, and the seminal vesicle has a lining of columnar epithelium. The cirrus sac is composed of an external muscular wall enclosing a mass of parenchymous tissue which surrounds the ejaculatory duct. This sac is very small in *P. integerrimum* and *P. hassalli.* Ventrally it opens into a common genital atrium (Fig. 26). The ejaculatory duct terminates in the genital papilla, which when retracted is surrounded by a deep depression. In the musculature between this depression and the wall of the cirrus sac are embedded the roots of the genital hooks. When the hooks are retracted there is a shallow depression between them and the wall of the sac. With the contraction of the wall of the cirrus sac the genital papilla and the circle of genital hooks are extruded thru the pore. In most of the species the hooks are sickle shaped with the points projecting outward, and with muscles attached to the outside of the hook at the juncture of the root and shank. These muscles undoubtedly serve as a fulcrum, and the extrusion of the papilla rolls the hooks outward burying their points in the cuticula lining the wall of the vagina of the copulating worm (Fig. 24). In *P. alluaudi* Beauchamp described three genital hooks, *P. integerrimum* has eight, and other species sixteen, thirty-two, and forty. In *P. hassalli* the genital hooks are small, straight and have a wing like process at the middle.

Zeller described a prostate gland in *P. integerrimum,* consisting of masses of large cells situated around the cirrus, and traced ducts from these cells to the lumen of the ejaculatory duct. Johnston in *P. bulliense* says, ''Two laterally placed, small groups of gland cells represent the prostate.'' The statement of Zeller that a gland is present around the cirrus of *P. integerrimum* is certainly correct. In the species described in this paper, a similar gland is present in the parenchyma around the genital sinus. The cells (Fig. 12) are globular or pyriform, stain deeply and possess a distinct nucleus and nucleolus. Their ducts could not be traced to the ejaculatory duct but in many cases appear to lead to the body wall near the margin of the genital sinus. In *P. orbiculare, P. opacum* and *P. megacotyle* the cirrus sac is large and many nuclei are present around the ejaculatory duct in the dorsal part of the sac. These nuclei are large, with distinct nucleoli, and are surrounded by a deeply staining area of granular or flaky substance, but no cell boundries could be made out.

Female Reproductive System.—In all known species but one, the ovary is oval or comma shaped. In *P. kachugae* it is described by Stewart as a ''curved sausage-shaped organ, the curve forming all but a complete circle. The fundus is somewhat bulbous.'' This structure is usually not more than one half the size of the testis, is situated a short distance anterior to that organ, and in a given species may lie on either side of the body. In all the species studied by the writer it is comma shaped, the larger part is ventral, anterior, and lateral, and terminal region is dorsal, posterior, and mesal. The ova are formed in the large part and the ovary is divided into zones of growth, ova of increasing size being present in each succeeding zone (Fig. 23).

In the species described in this paper the vitellaria consist of masses of follicles occupying the dorsal and lateral regions of the body. Each follicle consists of several cells which may vary much in appearance; the difference is due to the phase of secretory activity of the cells. In the peripheral part of the gland the cells are usually small, with granular or flaky protoplasm, a distinct nucleus and nucleolus; whereas those more centrally located may be two or three times their size, the extra-nuclear area being either vacuolated or filled with droplets of a yellow substance (Figs. 19, 20). In some cells the secretory droplets are scattered uniformly thruout the cell. The presence of the material in the cells often renders the body so opaque that the diverticula can not be seen. The glandular secretion is apparently identical with that which forms the shell of the egg, and this observation further confirms the statement of Goldschmidt (1909) that the so-called vitellaria secrete the shell of the egg. Small ducts from the follicles (Fig. 11) unite and discharge into longitudinal collecting ducts. These extend along the sides of the body, lateral to the ceca and dorsal to the excretory tubules; on either side of the body there is an anterior and a posterior branch which unite just behind the level of the ovary and the common duct discharges into the external end of the vitello-vaginal canal. In *P. bulliense,* Johnston reports: ''The lateral vaginal swellings are formed by a large number of papillae, perforated by fine canals, which after a very short course, open into a fairly wide sperm reservoir, situated one on either side, just under the swellings. From these reservoirs, a wide vaginal tube on either side runs backwards and inwards, to open into the anterior lateral yolk duct." A similar condition is described and figured by Zeller for *P. integerrimum.* In all other species in which the structure has been described, the vaginae are open funnels leading mediad and dorsad from their openings on the ventro-lateral surface of the body, and uniting just below the intestine with the common vitelline ducts to form the vitello-vaginal canals. The cuticular lining of the vaginae is very thick and in the parenchyma around the vaginae there are large cells of secretory type (Fig. 24). The vitello-vaginal canals lead medially and unite, either forming a duct which discharges into the ootype (Fig. 32) or opening separately into the ootype (Figs. 3, 16, 24).

From the ovary the oviduct passes posteriad and ventrad, opening into the ootype. Immediately anterior and dorsal to the opening of the oviduct, there branches from the ootype a small tube which after a somewhat twisted double loop opens into the intestine of the side in which the ovary is situated. This genito-intestinal canal has been the source of much controversy and its presence or absence is the diagnostic feature of Odhner's two groups of monogenetic trematodes. Mehlis' gland, the shell gland of earlier authors, is never largely developed and is difficult to find in some specimens where it is represented by a few nuclei in the parenchyma around the ootype. Zeller for *P. integerrimum* and Johnston for *P. bulliense* described prominent "shell glands", and Stewart for *P. kachugae* described "a group of glandular cells found at the same transverse level as the ovary, but on the opposite side of the midline. They appear to be connected with the corresponding vagina, but their function is obscure." Since they are in the precise location of the Mehlis' gland, one is led to suspect that Stewart was confused in regard to the connections and relations of this group of cells, altho in individuals of other species studied by the writer, there are groups of large glandular cells in the parenchyma surrounding each vagina.

The ootype is continued by a tube which passes anteriad on the opposite side from the ovary, and which leads to the uterus. Previous writers have called this tube the oviduct and Johnston (1912) says, "From the ootype, the oviduct runs forward to a point in front of the ovary, whence it bends sharply backwards and runs in a straight course close to the ventral surface, almost to the level of the cotylophore, where it opens into the wide uterus." The use of the term oviduct for the tube leading from the ootype to the uterus is confusing and objectionable. Looss (1899) says, "Der Theil des weiblichen Leitungswegen, der den Keimstock mit dem ootyp verbindet, ist der oviduct oder Keimgang," and this terminology is found in general use thruout the literature. In a large number of trematode genera the ootype opens directly into the uterus. In the Polystomidae however, there is a definite specialized tube leading from the ootype to the uterus. This duct is not homologous with the oviduct, it is separated from that duct by the ootype, and further, in the specimens examined by the writer the histological character of the two are not precisely the same. The epithelial lining of the oviduct is of the flattened type, and that of the second duct more columnar. Such a duct is present in many cestode genera and is called the uterine duct. The same name is proposed for the tube leading from the ootype to the uterus in the Polystomidae, altho with the understanding that its use is independent of the question of homologies of the female ducts in trematodes and cestodes.

In *P. bulliense* the uterine duct opens into the uterus not at the end but on the side, and there is a posterior uterine pocket. The uterus extends as a wide elongated sac from the extreme posterior end of the body to the common genital sinus. In *P. alluaudi* the intracecal area is occupied by the uterus and eggs are present almost as far posteriad as the caudal union of the ceca. In *P. integerrimum* there is a long uterus which extends in many loops anterior to the ootype, and contains a large number of eggs. In all other known forms, the uterus is situated at the level of the ovary on the opposite side of the body, and contains a single large egg or embryo. Zeller (1876) described a similar condition for the ectoparasitic form of *P. integerrimum*. Figure 14 shows a very early embyro of *P. orbiculare* and Figure 23 a much later stage of development in *P. megaeotyle*. No shell is present in the former case, altho it may have been lost in sectioning. There must be some provision for the growth of the embryo and the shell can not be rigid during the uterine period. Where the oviduct arises from the ovary, at its union with the ootype, and at either end of the uterine expansion sphincter muscles produce short contracted portions of the tube. In all the species studied by the writer, with the exception of the vitelline tubules, all ducts of the female system have a fibro-membranous wall and an epithelial lining, which in the ootype, uterine duct, and uterus consists of tall columnar cells with distinct boundries and single nuclei. Describing the epithelial cells lining the ootype in certain other monogenetic forms Goto (1894) says that because of their appearance and reaction to stains he strongly suspects their glandular nature, but since a shell gland is present he can not understand their function. In certain species of Polystoma Mehlis' gland is much reduced or absent, and in these forms the cells of the epithelial lining of the ootype appear to be secretive (Figs. 8, 9). This agrees with the present conception that the vitellaria secrete the shell substance and Mehlis' gland the fluid in which the eggs are suspended.

The genital pore is situated on the ventral surface in the median line, just posterior to the bifurcation of the digestive tract. It opens from a common genital sinus (Figs. 13, 26) into which the uterus discharges and thru which the cirrus is extruded. The opening from the uterus into the genital sinus is posterior and ventral, while the cirrus sac opens into the dorsal part of the atrium.

When the two specimens of *P. opacum* from *Trionyx ferox* were placed in a watch glass, they soon came in contact and immediately started copulation, the cirrus of each worm was inserted in the right vagina of the other, and the two worms attached to each other, both with the anterior suckers and those of the caudal disc that could be brought in position for adhesion. Attempts to separate the worms failed, so an effort was made to fix them in the copulating condition, but they separated on the application of the killing fluid. This explains the statement of Johnston: "On one side only, in the specimens sectioned, was the vaginal tube filled with sperms; that on the other side was empty." Benham (1901) and Mac Callum (1913) state that copulation in polystomes has been observed only by Zeller.

POLYSTOMA ORBICULARE Stunkard 1916

[Figures 1 to 14]

The material of this species consists of six specimens from the urinary bladder of *Pseudemys scripta* from Raleigh, North Carolina, one specimen from the urinary bladder of *Chrysemys marginata* from Chicago, Illinois, and two specimens from the urinary bladder of *Chrysemys marginata* from Creston, Iowa.

The body is an elongate oval, slightly more pointed anteriorly than posteriorly, and in two of the specimens with slight indentations of the body walls at the vaginae and at the posterior margin of the anterior sucker. These worms (Fig. 1) varied in length from 2.7 to 3.75 mm. and in width from 0.9 to 1.2 mm. The caudal disc is circular, 0.8 to 1.07 mm. in width, and bears the six suckers arranged symmetrically in a circle. The suckers are approximately 0.3 mm. in diameter, and are separated by regular equal intervals. No hooks could be found on the caudal disc with the exception of the single minute larval hooklet in the base of each sucker. These are 0.016 mm. in length and could be seen only under favorable conditions.

The anterior sucker (Fig. 6) is 0.25 to 0.27 mm. in length and 0.37 to 0.42 mm. in width. It opens into the pharynx, a spherical structure 0.24 to 0.28 mm. in diameter. There is a short esophagus visible in sagittal sections altho it is not distinguishable in toto preparations. The ceca meet anteriorly in a wide curve and extend as simple tubes almost to the posterior end of the body. They have no branches and terminate blindly. In caliber they vary from 0.04 to 0.116 mm.

The testis is spherical or oval, usually slightly longer than broad, and measures 0.29 to 0.39 mm. in width and 0.36 to 0.5 mm. in length. It is near or slightly anterior to the middle of the body. The sperm duct arises at its anterior margin and, lying dorsal to the ootype, passes anteriad. In front of the ovary it turns ventrad and expands into the seminal vesicle. At the outer end of the seminal vesicle the duct is encircled by a sphincter muscle, and then known as the ejaculatory duct passes thru the cirrus sac to open into the genital atrium (Figs. 3, 13). The cirrus sac is almost spherical, and consists of an external muscular capsule filled with parenchymatous tissue enclosing a central canal. In the dorsal part of the sac there are radial muscles passing from the wall to the central duct, and among these fibers a few large nuclei. More ventrally there are sets of muscles developed around the central duct and these are connected to the wall of the sac. Externally the central canal terminates at the apex of a papilla which is separated by a deep depression from the muscular ring that bears the hooks of the genital coronet. This conical muscular ring is protrusible and is separated from the wall of the cirrus sac by a second depression. The invaginations on either side of the genital coronet allow for the extrusion of the coronet of hooks with the genital papilla on the contraction of the wall of the cirrus sac, while the muscles attached to the central canal and the muscular ring bearing the genital hooks serve as retractors. The genital coronet consists of sixteen hooks, similar in size and shape; they have an external sickle-shaped part or shank which turns outward and a root or basal part of about the same length embedded in the musculature (Figs. 2, 13). The basal part is straight and hollow and the internal end is bifurcate. It bears many fine cuticular processes which are particularly prominent near its union with the shank. In the body parenchyma around the terminal part of the cirrus sac there are large unicellular glands (Figs. 12, 13).

The ovary is lateral and may be situated on either side of the body. It is 0.1 to 0.25 mm. anterior to the testis. It is ovoid in shape, with the larger part in which the ova are being formed anterior and ventral, and the oviduct arising from the dorsal posterior region. In sections it appears to be marked into zones, with larger and fewer cells present in each succeeding zone. It is 0.1 to 0.148 mm. in width, 0.14 to 0.185 mm. in length and in one specimen cut in cross sections 0.175 mm. in depth. The oviduct arises as a very small tube and immediately expands (Fig. 3). This expanded portion extends posteriad and ventrad and by means of a short constricted tube opens into the ootype, a specialized region of the female duct where the vitello-vaginal canals are received and the genito-intestinal canal is given off. The genito-intestinal canal twists in a double loop and then opens into the intestine of the side upon which the ovary is located (Fig. 10). The vaginae are ventro-lateral in position and open to the exterior by funnel shaped mouths. The vitellaria occupy the dorsal and lateral regions of the body; they extend anteriad to the pharynx and posteriad to the caudal disc. There is a strand of follicles across the dorsal side of the body just behind the pharynx, and then the follicles are entirely extracecal in the field anterior to the testis; posterior to the testis the vitellaria overlie the ceca and extend to the center altho they are scanty along the median line. Ventrally the vitellaria are entirely extracecal. Collecting ducts run longitudinally, laterad of the ceca; and just below the cecum of either side the common vitelline ducts formed by the union of the anterior and posterior longitudinal ducts unite with the internal ends of the vaginae to form the vitello-vaginal canals. These canals open directly into the ootype, one on either side, and are thus continuous, forming a canal thru the body from side to side. Mehlis' gland is represented by many nuclei which lie in the parenchyma around the ootype and uterine duct. This latter duct passes anteriad and laterad on the opposite side from the ovary; it is smaller than the ootype in diameter and the epithelial lining is lower. After a slight expansion it is constricted and then opens into the uterus. The uterus contained a single egg or embryo. Figure 14 shows a morula-like mass of cells found in one specimen; in the other specimens there were large spherical eggs, each enclosed in a yellow shell. They vary from 0.21 to 0.24 mm. in diameter.

The excretory system shows no departure from the typical form and while it can not be completely followed in sections, the larger ducts occupy the characteristic positions. The descending collecting ducts arise in the region of the anterior sucker and pass posteriad, lying lateral and ventral to the ceca. They wind back and forth in short curves and at the posterior end of the body turn anteriad and pass in the same winding course to the excretory vesicles. Both descending and ascending ducts receive small branches at irregular intervals. The excretory pores are lateral and dorsal, at the level of the bifurcation of the intestine (Fig. 7).

This species agrees with *P. alluaudi* in shape of caudal disc and absence of great hooks, but differs from that species in type of uterus, number of hooks in the genital coronet, and in the character of the intestinal diverticula and testis. *P. orbiculare* agrees with *P. hassalli* in the number of genital hooks, but the hooks are different in size and shape; *P. hassalli* has the great hooks of the caudal disc well developed whereas they are absent in this species. In certain particulars *P. orbiculare* resembles *P. opacum,* but the two species have different numbers of hooks in the genital coronets; they differ also in the relative size of caudal suckers. The great hooks of the caudal disc are present in *P. opacum.* The two species differ also in that one is parasitic in the urinary bladder and the other in the oral cavity.

POLYSTOMA OPACUM Stunkard 1916

[Figures 15 to 21]

Two worms of this species were obtained from the esophagus of a single specimen of *Trionyx ferox* from Newton, Texas, and another from the esophagus of *Malacoclemmys lesueurii* from the same region. These trematodes were the same color as the lining of the esophagus and so firmly attached that they were removed only with great difficulty.

The worms (Fig. 15) measured 4, 3.75, and 3.25 mm. in length and 1, 0.85 and 0.8 mm. respectively in width. The body has an elongate oval outline, is flattened dorso-ventrally, and observed in living condition, shows great variations in shape. In an extended condition it narrows at either or both ends, and the contracted form may be not more than half the length when extended, and broadly oval or quadrate in outline. The caudal disc is slightly wider than the body in the mounted specimens, measuring 1.09 and 1.21 mm. in width while each sucker is approximately 0.4 mm. in diameter. The suckers have a chitinous skeletal framework, as is described in the generic discussion. In the external meridinal band there are thirty-two divisions, which number corresponds to the number of hooks in the genital coronet. The suckers are arranged in a circle, altho the anterior pair are separated by a distance slightly exceeding that between the posterior pair. Between the anterior suckers there are many chitinous spicules, and in one specimen two of the larval hooklets. Chitinous spicules are present on the sides of all the suckers and over the ventral surface of the disc. Between the posterior suckers there are three pairs of hooks, viz. two pairs of the small larval hooks and one larger pair, but the great hooks are relatively much smaller than the corresponding hooks in other species in which they are present (Fig. 40). The larval hooklets are 7 to 9μ in length and the great hooks are 75μ in length. The chitinous spicules present on the disc have no definite arrangement and their points may stand in any direction; the three larval hooks between the anterior suckers of one specimen have no definite relative position and their hooks point in different directions; those at the posterior edge of the disc are set in a row at more or less regular intervals and their hooks all point backward.

The cuticular covering of the body is about 14μ in thickness, and on the contraction of the body is thrown into minute folds and furrows.

The anterior sucker is oval, 0.2 to 0.22 mm. in length and 0.23 mm. in width. It opens into the pharynx (Fig. 18), a spherical structure 0.3 mm. in width. There is a broad nerve commissure crossing the anterior part of the pharynx which contains large ganglion cells. From this dorsal commissure a nerve passes ventrad on either side of the pharynx.

The digestive tract is of the simple triclad type, the pharynx is followed by a short esophagus, 0.17 mm. in length in the sectioned worm, and the diverticula extend as simple tubes almost to the posterior end of the body. They are about 0.15 mm. in diameter and terminate blindly, dorsal to the middle pair of suckers (Fig. 21). The ceca are lateral but close together, separated by only 0.2 to 0.25 mm. They have the usual fibro-membranous coat and epithelial lining, and were empty in the sectioned individual.

The testis is spherical or slightly longer than broad in well extended specimens. It is slightly anterior to the middle of the body and is composed of a large number of lobes or strands of cells, compacted and enclosed in a membranous capsule. Cells with the chromatin of their nuclei in all stages of division and mature spermatozoa were observed in sections. The sperm duct arises at the anterior dorsal margin of the testis and curves dorsad and cephalad. Anterior to the uterus it turns ventrad and expands to form the seminal vesicle. From the seminal vesicle a small ejaculatory duct leads through the cirrus sac and opens into the common genital sinus.

The ovary is ovoid or comma shaped, situated a short distance anterior to the testis, and in all three specimens is located on the left side of the body; but since in other species it may lie on either side, it is probable that the examination of a larger number of individuals would show specimens with the ovary on the right side. In dorsal view it is from 0.16 to 0.2 mm. in length and 0.08 to 0.12 mm. in width, while in the specimen that was sectioned it is 0.08 mm. in width and 0.3 mm. in depth. The oviduct arises at the dorsal posterior margin and curves posteriad, mediad, and ventrad where it opens into the ootype. The vitello-vaginal canals open separately into the ootype, just ventral to the origin of the genito-intestinal canal. The latter duct passes laterad, then dorsad and anteriad, turns mediad almost to the median line of the body, then dorsad and laterad, and opens into the intestine of the side in which the ovary is located. The uterine duct passes to the right sight of the body, then dorsad and anteriad where it opens into the uterus. Mehlis' gland is present altho not well developed, and the cells are scattered along the uterine duct as well as around the ootype, altho they are not so numerous in the former as in the latter location. The vaginae open to the surface on either side at the ventro-lateral margins of the body, at the level of the posterior margin of the ovary (Fig. 16). On either side the inner ends of the vaginae unite just below the ceca with the common ducts from the vitellaria to form the vitello-vaginal canals. These open separately and directly into the ootype. The vitellaria consist of large compact follicles, underlying the entire dorsal surface of the body from the pharynx to the caudal disc, except the region over the ovary. The vitellaria are reduced and only a few follicles are present in the region over the testis and they are entirely absent in a circular area over the ovary. Ventrally the vitellaria do not extend mediad of the ceca. The vitellaria are so extensively developed that they obscure the internal structures and render the body opaque, and this character suggested the name of the species. Common collecting ducts run longitudinally along the body lateral to the intestinal diverticula and these discharge into the vitello-vaginal canals as previously described. In each of the specimens there is a single large egg in the uterus, and in the one sectioned the uterus extends cephalad of the genital pore and to a point 0.03 mm. from the bifurcation of the intestine. The eggs are broadly oval, 0.25 mm. long by 0.2 mm. wide. The shell is yellow, refractive to light, and apparently composed of the same substance that occurs in small droplets in the vitellaria.

The uterus and cirrus sac open into the genital sinus; the opening of the cirrus is anterior and dorsal to that of the uterus. The common genital pore is situated in the median line, about 0.12 mm. caudad of the bifurcation of the intestine. Embedded in the wall of the cirrus sac and with their points forming the so-called coronet, the genital hooks in appearance suggest the corolla of a flower. There are thirty-three of these hooks in one mounted specimen and thirty-two in the other. In entire length they measure 0.05 mm., the shank or projecting part comprising about half the total length.

P. opacum agrees with *P. alluaudi* and *P. orbiculare* in shape of caudal disc, but *P. alluaudi* has but three spines in the genital coronet, and a long post-ovarian uterus which contains many eggs. *P. orbiculare* has a larger anterior sucker, smaller caudal suckers, a smaller pharynx, fewer vitelline follicles, and only half as many hooks in the genital coronet. *P. opacum* differs from *P. coronatum* and *P. microcotyle* in the shape of the caudal disc and in the reduced condition of the great hooks of the disc.

POLYSTOMA MEGACOTYLE Stunkard 1916

[Figures 22 to 26]

The material of this species consists of three specimens from the mouth of *Chrysemys marginata* from Creston, Iowa. One worm was cut into cross sections and the other two mounted as stained toto preparations.

These worms (Fig. 22) have an elongate ovoid shape. Widest in the region just anterior to the caudal disc, they gradually become narrower anteriorly, and posteriorly they taper rapidly to a caudal tip which is set in the antero-central part of the caudal disc. The worms are 2.5 to 2.7 mm. long and 0.71 to 0.78 mm. in width. The caudal disc is cordiform and the suckers are so large that they slightly overlap each other. The suckers are arranged in about four-fifths of a circle around the lateral and caudal margins of the disc. Measurements thru the disc from side to side at the level of the cephalic suckers are from 1 to 1.4 mm., thru the middle pair 1.2 to 1.8 mm., and thru the caudal suckers 0.68 to 0.7 mm. The disc bears the characteristic armature of hooks. Across the anterior margin there are three larval hooklets in one specimen and four in the other, but their arrangement is not regular or definite and their position would indicate that they do not function in attachment. In the specimen reproduced in Figure 22 the two hooks of the right side have their points almost together and their bases apart. In the bases of the suckers there are small larval hooklets, and one pair similar in size and shape between the two caudal suckers. Also between the posterior suckers (Fig. 41) there is the pair of great hooks and a pair of hooks the same shape as the great hooks and intermediate in size between the great and larval hooks. The hooks measure in length: larval 0.017 mm., great hooks 0.116 mm., and the pair intermediate in size 0.058 mm.

The cuticular covering of the body is approximately 5μ in thickness on the dorsal and 3 to 4μ in thickness on the ventral surface. It is turned in at the external openings and lines the digestive tract to the bifurcation.

The anterior sucker is set off from the remainder of the body by a slight constriction. It is oval, its longest axis crosswise of the body, somewhat flattened posteriorly, and measures 0.28 mm. in length by 0.35 to 0.42 mm. in width. It is followed by the pharynx (Fig. 25) which is 0.35 to 0.38 mm. long, 0.38 to 0.44 mm. broad, and in the sectioned worm 0.34 thick. No esophagus was observed; the ceca meet anteriorly in a wide curve and extend almost to the posterior end of the body. They are 0.06 to 0.11 mm. in diameter, and have an epithelial lining 0.017 to 0.035 mm. in thickness set upon a fibro-membranous base. The vitellaria are so thick that the diverticula can not be traced in toto preparations.

The testis is situated near the center of the body; it is spherical or oval, 0.28 to 0.33 mm. long, 0.33 to 0.38 mm. wide, and in the sectioned worm 0.28 mm. thick. The course of the vas deferens and the character of the male organs are similar to those in the previously described species. The genital coronet contains thirty-six hooks in one and forty-two in the other toto preparation. They are similar in size and shape, have a straight basal portion with bifid end which is embedded in the wall of the cirrus sac, and a sickle shaped shank which projects into the genital atrium. The basal portion is the same length as the shank and each part measures 0.03 mm.

The ovary (Fig. 23) is a broad comma-shaped organ, situated about midway between the pharynx and testis, on either side of the body. The larger part is anterior and ventral and contains many nuclei of forming ova, and there are zones of developing ova, each with larger and fewer cells until dorsally and posteriorly the oviduct is given off. The oviduct passes mediad, expanding slightly, and then posteriad and ventrad to open into the ootype. This structure is in the ventral part of the body, just anterior to the testis (Fig. 24); from the sides it receives the vitello-vaginal canals and gives off the genito-intestinal canal. This canal after winding in a double loop opens into the intestine on the same side as the ovary. It was empty in the sectioned worm. The external openings of the vaginae are situated on small prominences ventro-lateral in position, altho there is a single large opening to the exterior. The vitellaria consist of masses of follicles occupying the dorsal and lateral areas of the body. They form a sheet of gland cells on the dorsal side of the body posterior to the testis. They are somewhat reduced along the median dorsal area in the anterior half of the worm and entirely absent only in small fields over the testis and uterus. They extend along the sides of the body and ventrally are limited by the ceca. On either side, at the level of the ootype, a common duct from the longitudinal collecting ducts passes ventrad and just below the cecum unites with the vagina of that side to form the vitello-vaginal canal which discharges into the ootype. The uterine duct leads to the uterus, which in each of the specimens contained a large egg. A section of the egg is shown in Figure 23. The eggs are oval, 0.15 by 0.18 mm., and in the sectioned worm the egg is 0.24 mm. in thickness. From the uterus a small duct passes anteriad and ventrad, opening into the genital atrium, posterior and ventral to the cirrus sac.

The excretory system agrees with the general description given.

The descending and ascending ducts are 6 to 11μ in diameter; when empty their walls collapse.

P. megacotyle differs from all known American forms in the large number of hooks present in the genital coronet, and in this character agrees only with *P. occllatum.* The species differs from *P. ocellatum,* however, in the difference in size of the anterior sucker and pharynx as well as in the size of the caudal suckers. *P. megacotyle* differs from *P. microcotyle* in the number of genital hooks and in the size of the posterior suckers. *P. megacotyle* has a larger pharynx, larger caudal suckers, and a larger number of gental hooks than *P. coronatum.*

POLYSTOMA MICROCOTYLE Stunkard 1916

[Figures 28 and 29]

This species is described from a single specimen from the mouth of *Chrysemys marginata* from Creston, Iowa. The worm was stained and mounted in toto (Fig. 28).

It is 3 mm. long, and 0.78 mm. in width. The caudal disc is cordiform, 1 mm. in width at the level of the anterior suckers, 1.07 mm. thru the middle pair, and 0.74 mm. thru the caudal pair of suckers. Each sucker is 0.28 mm. in diameter and with the exception of the longer distance between the anterior suckers, they are separated by almost regular equal distances. The distance between the anterior suckers is about four times as great as that between the posterior pair. Four larval hooklets are present between the two anterior suckers, three in a row but with their hooks pointing in different directions, and the fourth some distance posterior to the others (Fig. 29). Between the posterior suckers there are three pairs of hooks: the pair of great hooks, one pair of larval hooks, and a third pair intermediate in size between the great and larval hooks. The hooks of this third pair are the same shape as the great hooks. The larval hooks are 0.017 mm. long, the great hooks are 0.116 mm. long, and the pair intermediate in size are 0.061 mm. long.

In this specimen as the suckers are small the musculature of the caudal disc shows very plainly (Fig. 29). Muscle strands from the ventral side of the body and others from the body wall pass to the bases of each of the suckers. Others pass to the outside of the different suckers and are inserted on the distal and intermediate zones of the suckers, serving as retractors in the operation of the organs. Many break up into smaller fibers and can not be traced. From the base of each sucker the muscles spread out in a fan shaped manner and fibers can be traced not only to the large strands from the body wall but also small fibers pass from the base of each sucker to each of the other suckers. Many of the muscles branch and ramify thru the tissue of the disc.

The anterior sucker is 0.2 mm. long and 0.42 mm. wide; the pharynx is 0.37 mm. long and 0.4 mm. in width. No esophagus is visible in the single toto preparation and only the anterior part of the intestine can be seen.

The testis is slightly anterior to the middle of the body; it is oval, 0.36 mm. in length and 0.42 mm. in width. The sperm duct can be traced dorsally and anteriorly; cephalad of the ovary it expands into a seminal vesicle which stains deeply due to the presence of spermatozoa. The genital coronet contains thirty-two hooks, equal in size and similar in shape.

The ovary is on the left side of the body, about midway between the testis and the genital pore. The oviduct arises at the median posterior margin and passes mediad, but the structure of the ootype could not be made out. The uterus can be distinguished at the level of the ovary on the opposite side of the body and is empty. Laterally the vaginae are visible and the vitello-vaginal canals can be traced mediad a short distance from the ceca. The vitellaria are strongly developed, anteriorly they extend to the middle of the pharynx, and posteriorly to the caudal disc. There is a strand of follicles across the body from side to side between the pharynx and the level of the genital pore. The follicles occupy the dorsal and lateral regions of the body but anteriorly are reduced in the median area and are absent in the fields over the testis and ovary. They obscure the ceca caudal to the testis. No vitelline ducts were seen.

The excretory vesicles appear one on either side of the body dorsally, at the level of the bifurcation of the intestine.

In number of genital hooks this specimen agrees only with *P. coronatum* Leidy. A comparison with a type specimen of *P. coronatum* shows that in the latter form the pharynx and testis are much smaller and the suckers of the caudal disc are much larger.

POLYSTOMA CORONATUM Leidy 1888

[Figure 27]

This description was made from a single type specimen from the United States National Museum. The worm was stained and mounted in toto.

Leidy (1888) says the host is the common food terrapin, and the previous year, speaking of eating terrapin, he mentions *Emys palustris* and *Emys rugosa*. Braun (1879-1893) lists the species from *Cistudo* *carolina.* Goto (1899) in discussing the specimen described by Leidy as *P. oblongum*, refers to the food terrapin as *E. rugosa.*

Leidy gives no figure and his description states: "*Polystomum coronatum.* . . . . . Body when elongate lanceolate. Caudal disc wider than the body, cordiform, with three pairs of bothria and with the body attached between the anterior two pairs; changeable in form to oblong, circular or quadrate; with three pairs of minute hooks between the anterior part of bothria and with a larger pair and two smaller pairs between the last pair of bothria. Genital aperture with a circular or transverse oval coronet of thirty-two hooks of equal length. No eyes visible. Length, elongated from 4 to 6 mm; contracting to about half the length and widening proportionately."

The specimen from which the present description was made (Fig. 27) is 3.15 mm. long and 0.83 mm. in width. The greatest width is at the level of the vaginae; the body tapers rapidly anteriorly, widening again slightly at the anterior sucker. From the level of the vaginae the body gradually grows narrower posteriorly to its insertion into the caudal disc. The disc is 1.24 mm. wide at the level of the anterior suckers, 1.2 mm. thru the middle pair and 0.78 mm. thru the caudal pair of suckers. Each sucker is approximately 0.37 mm. in diameter, and constructed as previously described. There are thirty-two small divisions in the peripheral cuticular band of the only sucker in which they could be counted. The disc bears the usual eighteen hooks; the six larval hooklets at the anterior margin of the disc are situated in a row equidistant from the anterior edge of the disc, the two lateral hooks on either side are nearer each other than the more centrally located one is to the median one of that side. Larval hooklets are present in the bases of the suckers and one pair is present between the caudal suckers. Between the caudal suckers there are present also both a pair of great hooks and a third pair intermediate in size between the two. The larval hooklets are 0.02 mm. in length, the hooks of intermediate size are 0.051 mm., and the great hooks are 0.132 mm.

The anterior sucker is oval, 0.16 mm. long and 0.4 mm. wide; the pharynx is circular in outline, 0.3 mm. in diameter. No esophagus can be seen in the toto preparation and behind the posterior margin of the testis the ceca are obscured by the vitellaria.

The testis is slightly anterior to the center of the body, circular in outline, and 0.3 mm. in diameter. The vas deferens could not be distinguished; the cirrus sac in ventral aspect is 0.19 mm. in diameter; the genital coronet contains thirty-two hooks, similar in size and shape, the shanks being sickle-shaped.

The ovary is situated on the right side of the body, about its own diameter anterior to the testis; in ventral view it is circular, 0.094 mm. in diameter. The oviduct passes posteriad and mediad, and the ootype appears as a darkly stained area. The vaginae can be distinctly seen and laterad of the ceca on either side there is a large cavity communicating with the exterior. The uterus is empty; the folded walls of the cavity are visible on the left side of the body. The vitellaria are strongly developed. Masses of follicles occupy the dorsal and lateral regions of the body but ventrally do not extend mediad of the ceca. Anteriorly they extend to the region of the pharynx; there is a strand across the body just behind the pharynx and in the interceeal area anterior to the testis they are largely interrupted, permitting the structures in this region to be made out. None of the vitelline ducts are visible.

The excretory vesicles are anterior to and slightly laterad of the ceca at the level of the caudal margin of the pharynx, but no ducts could be seen.

POLYSTOMA HASSALLI Goto 1899

[Figures 30 to 33]

This species was described by Goto (1899) from the urinary bladder of *Cinosternum pennsylvanicum* from Maryland. The writer has since collected the species from other hosts and localities. A single specimen was found in the urinary bladder of *Aromochelys carinatus* from Newton, Texas; five were collected from the urinary bladder of *Aromochelys odoratus* from Raleigh, North Carolina; two from the urinary bladder of *Cinosternum pennsylvanicum* from Raleigh, N. C.; and three from the urinary bladder of *Chelydra serpentina* from Walker, Iowa.

The worms (Figs. 30, 31) vary from 1.3 to 2 mm. in length and from 0.4 to 0.65 mm. in width. The caudal disc varies in shape from hexagonal to cordiform and is of approximately the same width as the body. The suckers are 0.12 to 0.16 mm. in diameter. The eighteen hooks of the caudal disc have the usual arrangement and are described by Goto. However, he reports the larval hooks as being 0.33 mm. in length and the great hooks between the caudal suckers as 0.125 mm. in length. This is evidently a typographical error, since he figured the great hooks as about four times the size of the small ones. In the present material the great hooks are the same length as stated by Goto and the smaller ones are 0.033 mm. in length, which agrees with the figures of Goto by a change of one place in the decimal point.

The anterior sucker is ovoid, more pointed anteriorly. It may be longer in either the anterior-posterior or lateral axis and varies in diameter from 0.22 to 0.33 mm. The pharynx is spherical or oval and varies in width from 0.1 to 0.14 mm.; it may be longer in either axis. There is no esophagus, but in some specimens a median pocket of the intestine extends anteriad from the bifurcation to the pharynx. In others, and this is a more usual condition, lateral pockets of the intestine extend anteriad, one on either side of the pharynx (Fig. 33). The anterior sucker and pharynx are lined with cuticula; the intestine with the usual digestive epithelium. In those specimens in which the uterus contains an egg, the large size of the egg causes the ceca to be widely separated at the uterine level and they approach each other behind the uterus. In one specimen, median branches from the two ceca fuse and form a posterior connection of the diverticula (Fig. 30), and in another the two ceca are united at their ends.

The testis is situated ventrally, just behind the middle of the body. It is a somewhat shapeless mass, roughly oval in outline, crosswise of the body, extending between the ceca just posterior to the uterus. The vas deferens passes anteriad, dorsal to the ovary and between it and the uterus; anterior to the uterus the sperm duct turns ventrad, enlarges to form a seminal receptacle, and then passes thru the cirrus sac, opening into the genital atrium (Fig. 32). The cirrus hooks are sixteen in number, 0.028 mm. in length, straight, and with a wing like process at the middle as described by Goto.

The ovary is comma shaped or ovoid in outline, situated obliquely in the body, on either the right or left side. Typically the ovary is on one side of the body and the uterus on the other, but the enormous size of the egg causes the uterus to occupy a more or less central position, crowding the ovary far to one side. The ovary is 0.058 by 0.065 mm. in the smallest and 0.085 by 0.12 mm. in the largest worms, altho the size of the ovary does not correspond precisely with the size of the worm. The oviduct arises at the dorsal median and posterior part of the ovary and after a dorsal loop it turns posteriad and ventrad to open into the ootype. Mehlis' gland is present. The genito-intestinal canal branches from the ootype and after a short winding course opens into the intestine near the ovary. From the ootype, the uterine duct passes laterally to the opposite side of the median line and then anteriorly and dorsally to open into the dorsal posterior part of the uterus. The vitellaria extend from the pharyngeal region to the anterior margin of the caudal disc; there is a row of follicles across the dorsal surface behind the pharynx but they are absent between the ceca anterior to the testis. According to Goto, "lobes not very numerous, separated from one another, mostly confined to the lateral portion of the body, but also present in the median portion behind the testis." The vaginae are ventro-lateral, midway between the anterior and posterior ends of the body. There are no vaginal prominences, the vaginal openings are single, and internally they unite with ducts from the longitudinal vitelline ducts to form the vitello-vaginal canals, as described for the other species. They do not open separately into the ootype, but the two vitello-vaginal canals open into a common reservoir from which a duct passes dorsad and discharges into the ootype (Fig. 32). In a few of the specimens the uterus is empty and in others it contains a single large egg, the size of which varies within wide limits. The smallest eggs are 0.11 by 0.25 mm. and the largest 0.18 by 0.34 mm. The posterior edge of the uterus is at the level of the vaginae, and anteriorly there is a small duct from the uterus to the ventral posterior part of the genital atrium. The genital pore is in the median line, a short distance posterior to the bifurcation of the alimentary tract.

The excretory pores are slightly more posteriorly situated than in the previous described species. Descending and ascending ducts occupy the characteristic positions.

POLYSTOMA OBLONGUM Wright 1879

This species was described by Wright (1879) from the urinary bladder of *Aromochelys odoratus.* I have had no opportunity to work on material of the species and the following discussion is based on the description of Wright. According to that author *P. oblongum* measures up to 2.5 mm. in length and 1.5 mm. in width. The body is oblong in shape, tho capable of considerable variation. The caudal lamina is somewhat narrower than the greatest width of the body and is shorter than broad. The arrangement of the suckers and hooks is similar to that in *P. integerrimum;* the suckers are 0.2 mm. in diameter; the large hooks are 0.15 mm. and the small hooks are 0.015 mm. in length.

The mouth is on the ventral surface of the rounded anterior end. The pharynx is bowl-shaped and the intestinal ceca are without anastomoses or branches. The description of the excretory system is very meager; concerning it he says that only the convoluted lateral stems were observed near the anterior end.

The testis is situated in the posterior third of the body, the vas deferens passing dorsad and anteriad to the genital pore, which lies immediately behind the bifurcation of the intestine. The cirrus coronet is described as consisting of sixteen alternately large and small hooks. The free end of each is sharply curved, while the attached end is shaped like a cross the transverse piece of which is longer on one side than the other. The longer pieces measure 20μ and the shorter ones 15μ.

Doubt is expressed concerning the disposition and relations of the female organs. The ovary is described as situated in front of the testis on the right side of the body, but it seems probable that the organ figured as the "(shell gland?)" is really the ovary. The lobes of the vitellaria are scattered and extend from the pharynx to the caudal lamina or disc. It is doubtful whether Wright was correct in his statement that "The transverse duct seemed to pass inward dorsally from the intestinal ceca," since in all other known species the vitelline ducts are ventral in position.

The uterus is described as containing a single large egg or embryo. The egg shell is thin and is destitute of the short stump present in that of *P. integerrimum,* but has a rather large operculum. In two cases the embryo had already escaped from the shell and moved actively within the uterine chamber. It is a Gyrodactylus-like larva, similar to that of *P. integerrimum,* with eye spots disposed in the same fashion. It is devoid of cilia, and movement seemed to depend entirely on the muscles and hooks of the caudal disc. The latter had a rounded outline except posteriorly where there was a square projection bearing the four small posterior hooks. The disc measured 0.114 mm. across and the twelve small anterior hooks were disposed at regular intervals on the margin of the rounded part. There was no trace of suckers. The small hooks had already attained their definitive size and form. The two large hooks were situated considerably further in from the margin than in the adult, and measured only 0.024 mm. instead of 0.15 mm. in length, which difference it is stated was due to the shortness of the immersed portion, in which, however, the notch was already formed.

In shape, as well as relative position and size of organs, *P. oblongum* strongly resembles *P. hassalli.* It is significant also that both are from the urinary bladder of *Aromochelys odoratus. P. oblongum* is slightly longer and broader than *P. hassalli,* the posterior suckers are larger and the small hooks of the disc are only about half the length of those in those in *P. hassalli.* The two species agree in number of genital hooks, but in the former species the hooks are alternately large and small and with the free end sharply curved, while in *P. hassalli* they are straight and uniform in size.

The species in the genus Polystoma have been arranged in the form of an analytical key utilizing the more prominent or more useful diagnostic structures in separating the different forms. This key is found on the following page.

KEY TO THE SPECIES OF THE GENUS POLYSTOMA

1 (6) Uterus long, contains many eggs........ 2
2 (5) Great hooks present on the caudal disc........ 3
3 (4) Ceca branching .... *P. integerrimum*
4 (3) Ceca not branching .... *P. bulliense*
5 (2) Great hooks not present on caudal disc........ *P. alluaudi*
6 (1) Uterus short, contains a single egg........ 7
7 (22) Great hooks present on caudal disc........ 8
8 (21) Genital hooks of equal length........ 9
9 (12) Not more than sixteen genital hooks........ 10
10 (11) Genital hooks eight in number; ectoparasitic form .... *P. integerrimum*
11 (10) Genital hooks sixteen in number........ *P. hassalli*
12 (9) Genital hooks more than sixteen in number........ 13
13 (16) Genital hooks thirty-two in number........ 14
14 (15) Caudal suckers large, adjacent but not contiguous, pharynx, smaller than anterior sucker........ *P. coronatum*
15 (14) Caudal suckers small, widely separated, pharynx equal in size to anterior sucker .... *P. microcotyle*
16 (13) Genital hooks more than thirty-two in number........ 17
17 (20) Testis simple 18
18 (19) Caudal suckers large, overlap .... *P. megacotyle*
19 (18) Caudal suckers small, separated .... *P. ocellatum*
20 (17) Testis branched .... *P. kachugae*
21 (8) Genital hooks unequal in length........ *P. oblongum*
22 (7) Great hooks of caudal disc reduced or absent........ 23
23 (24) Genital hooks sixteen in number........ *P. orbiculare*
24 (23) Genital hooks thirty-two in number........ *P. opacum*

ASPIDOGASTRIDAE

Because of its peculiar multiloculate adhesive apparatus, Burmeister (1856) called attention to the difference between the genus Aspidogaster and the remainder of the trematodes, and suggested a division of the Trematoda into (1) Malacobothrii for the distomes and holostomes, (2) Pectobothrii for the polystomes, and (3) Aspidobothrii for Aspidogaster. Subsequent writers however continued to include Aspidogaster with the polystomes until Monticelli (1892) revived the classification of Burmeister, but named the three suborders into which he divided the trematodes, Heterocotylea, Aspidocotylea, and Malacocotylea.

In the classification of Monticelli, the Aspidocotylea contained the single family Aspidobothridae. Poche (1907) proposed to make the name of the family agree with the rules of zoological nomenclature according to which "The name of the family is formed by adding the ending -idae to the stem of the name of its type genus." Thus the name of the family must become Aspidogastridae.

The family is of special interest to students of trematode morphology. The form of the adhesive apparatus, with its retractile marginal organs, the separation of the body into dorsal and ventral portions by a muscular partition, the sac-like alimentary tract, and the details of the genital organs are peculiar to the group. The family contains both ectoparasitic and endoparasitic species, forms with direct development and at least one species which has an intermediate host, while the hosts infested by the adult parasites include both invertebrates and vertebrates, species having been reported from molluscs, fishes, and turtles.

Summaries or revisions of the group have been made by Diesing (1850, 1859), Taschenberg (1879), Hoyle (1888), Monticelli (1892), Braun (1879-1893), and Nickerson (1902).

Only three species representing two genera of the family are known from North America, *Aspidogaster conchicola* von Baer 1827, *Cotylaspis insignis* Leidy 1856, and *Cotylaspis cokeri* Barker and Parsons 1914. Representatives of each of these species were available for the present study. The first two species are well known; concerning *A. conchicola* no further data were obtained, but a few corrections are made to former descriptions of *C. insignis*.

Cotylaspis cokeri has been mentioned but once in print, but on the basis of extended studies this form had been fully described and its position as a new species demonstrated in a thesis submitted by the writer in partial fulfillment for the degree of Master of Arts in the Graduate school of the University of Illinois in June 1914. The following October Barker and Parsons (1914), having also been working on this form independently, published a brief description naming it *Cotylaspis cokeri*. Since I had completed my work on it before the appearance of their note and the publication of their final report has been delayed it seems proper to give here a detailed description of the species.

ASPIDOGASTER CONCHICOLA von Baer 1827

About fifty specimens from the pericardial and renal cavities of *Andonta corpulenta* from Havana, Illinois, and a similar number of specimens from the same organs of *Quadrula undulata* from North Judson, Indiana, constitute the material of this species available for study.

A detailed comparison of these specimens with the descriptions of *A. conchicola* as given by Voeltzkow (1888), Stafford (1896), and other writers, shows that they belong to that species and substantiates the observations of Leidy (1851), Kelly (1899), and Kofoid (1899), that *A. conchicola* occurs in this country. So far it is the only species in the genus known from molluscan hosts.

Kelly (1899) made a parasitological examination of 1537 individuals of forty-four species of unios from Mt. Vernon, Iowa, Havana, Illinois, and Lewisburg and Phoenixville, Pennsylvania, and included in his report results of the examination of seventy-seven individuals belonging to eighteen species, made by Kofoid in 1895 and 1896. In four hundred thirty-five cases *A. conchicola* was found in the pericardium only, in seventy-five in the kidneys only, and in one hundred thirty-four cases both cavities contained the parasite. The presence of the mature trematode in the pericardium and of eggs within the nephridia was not infrequent. Of the 1537 specimens examined, forty-one per cent were parasitized with *A. conchicola* and thirty-seven of the forty-four species were infested with the parasite.

No further data on this species were obtained by the present study.

COTYLASPIS INSIGNIS Leidy 1856

[Figure 56]

The material of this species consists of specimens from *Anodonta imbecilis, A. corpulenta, Lampsilis gracilis,* and *Unio pustulosis* from Havana, Illinois, and others from *Anodonta ferrus* and *A. ovata* from Reed's Lake near Grand Rapids, Michigan. The material proved to belong to the same species and was identical with *C. insignis* Leidy.

Leidy first discovered the parasite in the Unionidae of the Schuylkill River and founded the genus to receive the new species. His generic and specific diagnosis (1858) follows: "Body curved infundibuliform, anteriorly cylindro-conical, posteriorly expanding into a subcircular or oval ventral disc with numerous acetabula arranged in a triple series. Mouth infero-terminal, with prominent upper lip, and protractile into a cup or disc like acetabulum. Intestinal apparatus as in Aspidogaster, eyes two, distinct, black, situated on either side of the head. Generative apertures inferior between the head and ventral disc."

According to the same author, *C. insignis*, the type species is: "Translucent white or pink white, upper lip snout like, conical, ventral disc crenate at the margin: acetabula twenty-nine, oblong quadrate, the outer rows continuous in front and behind forming a circle. Length from one-half to one line; ventral disc from one-fourth to one-half line in diameter. Adheres to the outer surface of the renal organ and upper margin of the foot, within the cleft of the upper branchial cavity of *Anodonta fluviatilis* and *A. lacustris.*"

Forbes (1896) reported this parasite in the river clams at Havana, Illinois. Osborn (1898) described the species from Lake Chautauqua, New York, as *Platyaspis anadontae.* Kofoid (1899) corrected this error, demonstrating that Leidy's genus is entitled to recognition, and establishing the specific identity of *Platyaspis anadontae* Osborn with *C. insignis* Leidy. Kelly (1899) reporting on the examination of over sixteen hundred individuals of forty-four species of Unionidae found the parasite in twenty-four different species of molluscs and in eighteen per cent of the individuals examined.

Osborn (1904) gives a review of the literature, an account of the distribution, habits, external and internal anatomy of the mature worm, and a description of a very young individual. The young specimen described has a simple ventral sucker, no eye spots, no marginal organs, two entirely distinct excretory systems, and wholly separate pores. This condition of the excretory system is compared with the condition in redia and cercaria and according to Osborn favors the idea suggested by Leuckart that the Aspidogastridae are sexually mature redia.

COTYLASPIS COKERI Barker and Parsons 1914

[Figures 46 to 55, 57, 58]

From four to twenty-five specimens were found in the intestine of each of seven specimens of *Malacoclemmys lesueurii* from Newton, Texas.

The worms (Figs. 46, 47, 52) average 1.5 mm. in length by 0.7 mm. in width, altho there is considerable variation in relative length and width due to the movements of the animal. The body is composed of two parts, an anterior dorsal forebody and a posterior ventral adhesive disc. When extended (Fig. 46), the forebody has the shape of a cornucopia, the larger end attached obliquely to the central two-thirds of the dorsal surface of the adhesive disc. In this condition the worm has an elongate form, projecting beyond the adhesive disc a distance equal to the length of that structure: in a retracted condition (Fig. 52) it is compact and may not project beyond the disc. The total length of the worm varies therefore with the state of extension of the forebody, from the length of the adhesive disc to twice that distance.

The adhesive disc (Figs. 47, 57) is a muscular organ, a multiloculate sucker, used for attachment and locomotion. It has a crenate oval outline, the dorsal surface is arched, and the ventral surface is flattened. The ventral surface is divided by two longitudinal and eleven cross ridges into thirty-two acetabula, which are arranged in three rows; there are twenty-two peripheral alveoli enclosing ten median alveoli. In this statement, the alveolus at either end is counted in the peripheral rather than the median row, tho in location included in both. These compartments change in shape with the movements of the animal, becoming oval or quadrangular. The shape and size of the disc are relatively constant, measurements of the disc in twenty mounted toto specimens vary only from 1.2 to 1.4 mm. in length and from 0.58 to 0.78 mm. in width. This structure recalls the molluscan foot, and it has often been termed the foot altho the morphological comparison is not precise.

Movement consists of extension of the forebody, which furthermore may be turned in any direction, and in the less striking and more restricted movement of the disc. The disc has a tendency to turn up at the edges, especially at the anterior and posterior ends. In adhesion the organ may act as a unit, or the separate alveoli may function independently. In locomotion there is a regular series of movements, the forebody is extended and attached by the sucking action of the mouth funnel, then the disc is loosened and the forebody contracted, bringing the anterior part of the disc near the mouth, when the disc is attached and the series of movements repeated. The worm moved rapidly across the field of the microscope.

Body Covering.—Externally the worms are covered by a non-cellular cuticula, which is thickest on the dorsal side of the body and thinnest on the ventral surface of the adhesive disc (Figs. 49, 53). It is without hooks or spines, and on the dorsal surface reaches a thickness of 5μ, while on the ventral surface of the disc it is only about 1μ in thickness. The cuticula is turned in at the external openings and lines the external portions of the canals of the alimentary, excretory and reproductive systems.

Musculature.—Immediately inside the cuticula is the three layered dermo-muscular wall, circular longitudinal and oblique muscles occurring in the order mentioned, the circular lying next to the cuticula and in all parts of the wall being better developed than the others. The musculature is delicate and in some places the longitudinal and oblique muscles are very scanty. The musculature of the ventral side of the forebody is continued posteriorly in a thin sheet, the so-called septum or diaphragm (Fig. 53), which lies just above the limiting membrane of the musculature of the disc and extends posteriad as far as the caudal end of the cirrus sac. In *C. insignis* Osborn described this structure as passing posteriad as far as the caudal end of the ovary and in other genera it is more strongly developed. The parenchymous muscles of the body are long, often much branched, and most abundant in locations where they connect different parts of the body wall with each other or with adjacent internal structures. In the anterior part are many well developed muscles of this type used in the movement of that region. Running longitudinally among the vitellaria, as well as dorso-ventrally among the viscera there are many muscle fibers. Sphincters and dilators occur at the genital pore, excretory pore, at the base of the mouth funnel, and at the opening between the pharynx and the intestine.

The disc is separated from the forebody by a limiting membrane (Figs. 49, 53). This membrane runs parallel to the general course of the external ventral surface of the disc, projecting ventrad at each ridge. Extending between this membrane and the external wall there are muscle fibers, often much branched especially at the ends. The ventral projections of the limiting membrane into the ridges of the disc form two sides of long triangular prisms, which extend longitudinally and transversely above the musculature of the disc. One face of each of these prisms is dorsal and the opposite angles extend ventrad forming the ridges which separate the disc into fossettes. These ridges are composed of fibrous connective tissue in which a few nuclei are embedded.

Alimentary Tract.—The mouth funnel is a cup shaped muscular structure (Fig. 51) which functions as an organ of adhesion. There is no oral sucker. The mouth funnel is 0.08 to 0.1 mm. in diameter, sub-terminal in position. There is no prepharynx, the mouth funnel opens directly into the pharynx. The latter is a spherical muscular organ 0.09 to 0.1 mm. in diameter. As described by Osborn for *C. insignis*, it is followed by a very short esophagus, which in the anterior part has a cuticular lining and in the posterior part where the esophagus passes over into the intestine, a lining of flattened epithelial cells. The intestine is an elongate sac or tube extending on the dorsal side of the body 0.1 to 0.2 mm. posterior to the caudal edge of the testis. It varies but slightly in caliber, averaging about 0.075 mm. in diameter. The wall consists of a fibro-membranous sheet upon which rests a layer of columnar epithelial cells. The large deeply staining nuclei of the epithelial cells lie in the basal part while many delicate elongate processes extend out into the lumen of the canal.

Male Reproductive Organs.—The testis is large, single, median, its anterior margin lying at the center of the adhesive disc. It is almost spherical and measures 0.25 to 0.35 mm. in diameter. Cells of various sizes and with the chromatin material in various stages of division, as well as mature spermatozoa are to be seen in sections. The sperm duct arises at the anterior part of the testis and turns to the left, entering the side of a long, much-coiled seminal vesicle (Fig. 48). This vesicle is a large tube, 0.1 to 0.175 mm. in diameter, extending from the region of the testis to the cirrus sac. It is coiled eight to sixteen times and in all mature specimens is filled with spermatozoa. Terminally it is constricted into a small tube which enters the large cirrus sac. This latter structure (Fig. 53) is 0.145 to 0.2 mm. wide and 0.2 to 0.25 mm. long, has a strong muscular wall, and is pyriform in shape, the smaller end opening anteriorly at the genital pore. Inside the cirrus sac there is a dilated, curved portion of the duct which has muscular walls and is lined with epithelial cells. Surrounding the duct and filling the cirrus sac are the large cells of the prostate gland. These are pyriform and average 26μ long by 17μ wide. In living specimens the cirrus was observed in the extruded condition.

Female Reproductive Organs.—The ovary is a small organ, ovoid in shape, averaging 0.16 mm. in length, 0.1 mm. in width, and 0.05 mm. in thickness. It is located (Figs. 46, 52) at the right of the median line, slightly anterior to the middle of the body. The oviduct arises (Fig. 48) at the posterior ventral margin of the ovary and passes posteriad; receives a short common vitelline duct, and then expands into two or three irregular enlargements. Mehlis' gland is present, the nuclei lying in the parenchyma around the ootype. The uterus passes posteriad on the lateral side of the collecting duct of the excretory system as far as the caudal end of the testis where it turns to the median line. It passes ventrad and anteriad beneath the testis; in front of the testis it turns dorsad and toward the ovary, but just before reaching the ovary it turns and crosses to the opposite side of the body and then passes with little deviation to the genital pore. There is a strong sphincter at the distal end of the uterus (Fig. 54). Eggs were present at various places in the course of the uterus and when the worms were placed in tap water, the eggs near the pore were extruded. The eggs are few in number, not more than six being present in any specimen. They vary from 0.071 to 0.086 mm. in width and from 0.137 to 0.145 mm. in length. The average of twenty-five is 0.075 by 0.141 mm.

The vitellaria (Figs. 46, 49) are arranged along the sides of the body, extending from the posterior end to the level of the cirrus sac. The follicles are more numerous and closer together in the posterior region, gradually becoming fewer in the anterior part of the vitelline zone. They lie just above the limiting membrane which forms the dorsal boundary of the musculature of the adhesive disc, and number up to forty on each side. They vary in size, measuring from 10 to 40μ in diameter. In some specimens they appear to be arranged in a double row on each side with the follicles placed alternately, but there is common and wide variation from this condition. Collecting ducts extend along the median face of the vitellaria and at the level of the ootype pass mediad where they unite to form a small receptacle which empties into the ootype. In *C. cokeri* the vitelline follicles are smaller and fewer in number than in *C. insignis.*

The genital pore (Fig. 54) is double, situated in the median line on the ventral side of the forebody, dorsal and anterior to the adhesive disc. There is no genital atrium, the two ducts open to the exterior separately, the opening of the cirrus sac is on the right and that of the metraterm is on the left. Barker and Parsons described a genital atrium opening thru a common pore, but I fail to find such a structure. In *C. insignis,* Osborn described a single genital opening and a genital atrium, but in sections of *C. insignis* I find the same condition as in *C. cokeri.*

Excretory System.—Most of the observations on this system were made on living specimens. As the water evaporated from under the coverglass the worm was flattened and the larger excretory tubules could be easily followed. The pore (Fig. 50) is median, dorsal, near the posterior end of the body. There may or may not be a small papilla-like prominence around the pore. There is a single excretory vesicle, situated between the large flask like ends of the collecting ducts and the pore. In the pulsations of this organ, the anterior ventral part contracted and the constriction passed posteriad and dorsad, expelling the fluid thru the pore. The two collecting ducts extend cephalad from the excretory vesicle, one on either side of the forebody, median to the vitellaria. Just posterior to the pharynx each duct divides, sending a branch cephalad on the lateral side of the pharynx and anterior sucker, and a second branch turns caudad. This caudal branch subdivides into a branch leading to the region of the genital pore, and a longer larger branch which passes posteriorly to the region of the testis and receives many smaller side branches. Cross sections (Fig. 49) show the collecting ducts to be dorsal in position. In morphological and histological features the excretory system of *C. cokeri* is similar to that of *C. insignis*. Osborn gives a comparison of the excretory system in that species with the same system in other genera of the family.

Sensory Structures.—There is a dorsal nerve commissure crossing the anterior part of the pharynx, and nerves were traced running cephalad and caudad from it. In about half of the specimens mounted in toto, a pair of black pigment spots is present on the dorsal commissure. In others only a single spot is visible and in a few specimens none could be found. In all the sectioned worms, however, both ''eye spots'' were observed, altho in some they were very small and difficult to find. These structures are dorsal and anterior to the pharynx (Fig. 58) and consist of a large number of black pigment granules. No lens is present. Barker and Parsons report that eye spots were not found.

At the ends of the cross partitions of the adhesive disc are the marginal organs (Fig. 55). These structures occur in the interstices between the muscular ridges of the ventral disc and its peripheral wall. Such an organ consists of a fine tube about 20μ in length and 1μ in diameter, leading dorsad from the ventral surface of the ridge and terminating in a large spherical cavity in the form of a bulb. The entire organ is lined with cuticula, continuous with that of the external surface of the body. The external half of the canal possesses a thick wall composed of annular muscles, while the internal portion has a thin wall with a few annular fibers and is often curved or looped. At the external end of the inner portion there is a flask-like enlargement which is connected with the heavy walled region by a short constricted portion about 2μ in length. Longitudinal fibers pass from the wall of the distal part of the canal to points near its inner end or to the wall of the cavity. This latter structure is spherical or oval 15 to 20μ in diameter, and empty in most of the sections. It has a fibro-membranous wall and in a few cases is filled with homogenous granular substance or fluid. In other sections the bulb contains a few granules or "concretionary bodies", but in structure these appear identical with the cuticular lining of the cavity. As mentioned above the organs are located in the angles between the muscular ridges and the wall of the disc, and are set in a mass of non-staining fibrous connective tissue. Some of the fibers pass dorsad from the bulb between the muscular ridges to the limiting membrane of the disc, but in appearance these are similar to the others and there is nothing to indicate that they are nervous in character. However in one section, stained with Heidenhain's iron haematoxylin, there is a nerve fibril passing around the bulb and terminating on the inner end of the heavy walled portion of the canal (Fig. 55). Other nervous structures were not observed. The connective tissue contains many nuclei, similar in size and shape, and in no case was a connection between these nuclei and the marginal organ observed. No glandular cells and no evidence of a secretion were found. In the study of living specimens it was noted that the marginal organs were everted and retracted as the worm moved. Everted they appeared as membranous sacs and their movement was rapid and precise. No evidence was found to indicate that these organs possess a glandular function; the character of their movement and the nerve fibril leading to the canal as demonstrated incline the writer to regard these structures as sensory.

Similar organs have been reported as present in all the genera of the family except Stichocotyle. They were first noted in Aspidogaster by Dujardin (1845) who described them as pores or orbicular glands. Voeltzkow (1888) observed in Aspidogaster that they were protrusible and retractile, and for this reason decided they were sensory. Monticelli (1892) described them in *Cotylogaster michaelis* and supported the idea of their sensory character. Nickerson (1902) described in *Cotylogaster occidentalis* a bundle of fibers which he regarded as a nerve entering the bulb at its basal end, and a cluster of bipolar nerve cells lying upon the side of the bulb against which the canal is coiled when retracted. He stated that the presence of the bipolar cells establishes the sensory character of these organs. He described the bulb as filled with vesicular or granular material, and tho no nuclei were discernible, regarded this as cytoplasm of granular cells in different stages of activity.

Looss (1902) in *Lophotaspis vallei* described two types of structures as occurring in the interstices between the muscular ridges of the ventral disc. Those around the periphery of the disc at the ends of the cross ridges he called "marginal bodies" and those at the intersections of the ridges he called "tentacles." The first he compared with the marginal organs of other aspidogastrid genera, and the tentacles differ only slightly in details of structure. He stated there was nothing in the structure of the marginal bodies to warrant the former belief in their sensory character. Granules in the cavity he regarded as droplets of a secretion; and in the connective tissue dorsal to the cavity he described sac-like spaces with fine granular contents, and he found also nuclei but was uncertain whether they lay in the spaces or between them. The marginal bodies he regarded as glandular organs altho doubtful as to their exact function. He described the tentacles as having a spindle-shaped cavity with glandular apparatus around the inner end, and a canal leading from this blind end to the limiting membrane which formed the dorsal wall of the musculature of the adhesive disc. He considered these structures as adhesive or absorptive, but states that their physiological significance was doubtful.

Osborn (1904) in *C. insignis* described the marginal organs as consisting of three parts, the canal with its muscular wall, the cavity, and a dorsal fibrous part. The fibrous part he regarded "as a trunk of nerve fibers running at least to the muscles of the organ and perhaps partly sensory as well." The central cavity possessed "a lining of moderate thickness composed of cuticle outwardly but of nucleated epithelium on the inner side." This cavity he found empty or with one or more "concretionary objects." He says, "This indicates that secretion is going on the products being removed from time to time. I think the muscles described above may be used in discharging these products, the longitudinal fibers may act as dilators of the outlet, needed to enable such large objects to make their escape." Later he states, "I do not find in Cotylaspis any evidence of a glandular structure in the fibrous part, and do consider the bulbous part as epithelial and secretory."

The marginal organs apparently differ somewhat in structure in the different genera. Of all the authors, Looss alone seems to have morphological evidence for his conclusion that in Lophotaspis they are glandular in character. The statement of Osborn that in *Cotylaspis insignis* the bulb is partly lined with cuticula and partly with secretive epithelium, I regard as doubtful. Certainly in my sections of that species (Fig. 56) the bulb is lined with cuticula thruout. In the dorsal part of the cavity shown there are many small structures but they appear to be composed of the same material as the lining cavity. If they are cuticular, this would argue against the glandular character of the organ since in its functional activity the material would be swept out with the secretion instead of accumulating and forming such large objects as he shows in his figure. Furthermore it would be almost if not entirely impossible for such large bodies to pass thru the small canal which leads to the exterior. These "concretionary objects" are apparently the only basis for Osborn's claim that the organs are glandular since he stated that he found no glandular structure in the fibrous part. Instead of supporting I believe that they are subversive to the idea of the glandular nature of the organ.

In my material the fibers which pass dorsad from the bulb are identical in appearance with the adjacent connective tissue and do not appear to be nervous. The muscular wall of the canal is I believe, used primarily in the eversion and retraction of the external part of the canal. In living specimens under observation the everted part of the marginal organ was about the size and shape of the thick-walled distal portion of the canal, and this is probably the only part protrusible. With this eversion, the base of the thick walled portion to which the nerve is distributed would be at the tip of the everted structure in a position to function in a sensory capacity.

Comparisons.—This is the third aspidocotylean described from turtles, the two previously reported forms being *Cotylaspis lenoiri* Poirier 1886, and *Lophotaspis vallei* Stossich 1899, both African species. Poirier described *C. lenoiri* from the intestine of *Tetrathyra vaillanti* from Senegal, and Looss (1902) reports it as occurring also in*Trionyx notilica* of the Nile. *Lophostaspis vallei* is parasitic in the stomach of *Thalassochelys corticata*. *Cotylaspis cokeri* is very different from Lophotaspis, but shows considerable resemblance to *C. lenoiri*. However, a comparison of the description of *C. lenoiri* with specimens of *C. insignis* and *C. cokeri* shows decided difference in the size and shape of the worms and of the adhesive disc, in the number of alveoli and marginal organs, in the sive of ovary and testis, of cirrus sac, and of eggs. The three forms agree in essential morphological features and fit the diagnosis of the genus Cotylaspis as given by Leidy, but are equally clearly good species in that genus.

CLASSIFICATION OF THE FAMILY

The last classification of the Aspidogastridae was made by Nickerson (1902). Since additions and changes have subsequently been made, further revision seems advisable. The present arrangement is largely based on the work of Nickerson and brings the classification to date. Present information supports the validity of the following genera.

I. Aspidogaster von Baer 1827. Type species, *A. conchicola* von Baer.

Oval adhesive disc, four rows of alveoli, marginal organs present, mouth subterminal, no oral sucker, one testis.

This genus contains *A. conchicola* which infests the pericardium and renal organs of various species of Unionidae in Europe and North America. It is also found in gastropods and in the immature condition in the intestine of Unionidae. Other species of this genus are *A. limacoides*

Diesing 1834 from the intestine of a fish (Leuciscus) in Europe, a form which Stafford (1896) and Kofoid (1899) suspect of being identical with *A. conchicola*. The species *A. macdonaldi* was placed in this genus by Monticelli (1892) and removed to Lophotaspis by Looss (1902). Linton (1905) described *A. ringens* from the intestine of *Micropognon undulatus* and *Trachinotus carolinus* at Beaufort, North Carolina. MacCallum and MacCallum (1913) gave a more complete description of *A. ringens* and described *A. kemostoma* n. sp., both from the intestine of *Trachinotus carolinus*.

II. Cotylaspis Leidy 1857. Type species, *C. insignis* Leidy.

Oval adhesive disc, three rows of alveoli, marginal organs present, mouth subterminal, no oral sucker, one testis.

This genus contains the species *C. insignis, C. lenoiri*, and *C. cokeri*. *C. lenoiri* was described by Poirier (1886) as a species of Aspidogaster. Monticelli (1892) created a new genus Platyaspis to contain Poirier's species, evidently overlooking the similarity between it and the form reported by Leidy. He declined to accept the genus Cotylaspis, suggesting that *C. insignis* was a species of Aspidogaster. Braun (1879-1893) ascribed the species to Aspidogaster. Kofoid (1899) established the validity of Leidy's genus but contended that the genus Platyaspis should be retained for Poirier's species. Nickerson (1902) argued that the differences between the African and American species are not of generic importance and suppressed the genus Platyaspis, making *Aspidogaster lenoiri* Poirier and *Platyaspis lenoiri* (Poir. 1886) Monticelli 1892, synonomous with *Cotylaspis lenoiri* Poir. *Cotylaspis insignis* occurs ectoparasitically in the mantle cavity of Unionidae in North America; *C. lenoiri* is from the intestine of *Tetrathyra vaillanti* of Africa; and *C. cokeri* is from the intestine of *Malacoclemys lesucurii* of North America.

III. Macraspis Olsson 1868. Type species, *M. elegans* Olsson.

A single row of confluent acetabula in adhesive organ, marginal organs present, mouth terminal, one testis.

The single species is parasitic in the gall bladder of *Chimaera monstrosa*. a fish from the coast of Europe.

IV. Stichocotyle Cunningham 1884. Type species, *S. nephropis* Cunningham.

A single row of more or less distinct acetabula, marginal organs lacking, mouth subterminal, oral sucker absent, two testes.

Cunningham's original description was of the larva and Monticelli (1892) declined to recognize its generic importance, thinking it might be a form of Macraspis. Odhner (1898) by discovering the adult and tracing the life history, established the genus. Adults live in the bile ducts of the liver of rays; larvae occur encysted in the wall of the intestine of the larger marine Crustacea. Cunningham described it from the Norwegian lobster, Nephrops, and Nickerson (1895) reported it from the American lobster, *Homarus americanus.*

V. Cotylogaster Monticelli 1892. Type species, *C. michaelis* Monticelli.

Adhesive disc with three rows of alveoli, marginal organs present, mouth terminal, oral sucker present, two testes.

Two species have been described; *C. michaelis* occurs in the intestine of *Cantharus vulgarus*, a European fish, and *C. occidentalis* Nickerson 1899 is parasitic in the intestine of *Aplodinotus grunniens* of North America.

VI. Lophotaspis Looss 1902. Type species, *L. vallei* (Stossich) 1899.

Adhesive organ with four rows of alveoli, marginal organs present at all the intersections of the ridges of the adhesive disc, cirrus absent.

Loos in 1901 reported *L. adhaerens* as belonging to a new genus of the Aspidogastridae, but was not aware that Stossich two years before had described the same form as *Aspidogaster vallei.* Looss later (1902) described and figured the form under the name of *Lophotaspis vallei.* In the same paper he compared *A. macdonaldi* with *L. vallei* and placed the former species in the genus Lophotaspis. This trematode was reported but not named by Macdonald in 1878, and named by Monticelli (1892) as a species of Aspidogaster. Nickerson (1902) declared it to be an aspidogastrid, but different from all other known species, and predicted that a new genus would have to be erected for it when its structure was better known. Macdonald reported one hundred eighty extensile structures, like the tentacles of a snail, occurring at the margins and intersections of the ridges of the adhesive disc. Nothing is known of the internal structure. Looss in placing the form in the genus Lophotaspis stated: "Mit ihrer tentakeltragenden Bauchscheibe bildet die Art aber ganz zweifellos einen fremden Eindringling in der Gattung Aspidogaster, da dessen typischen Art jedenfalls solche Tentakel nicht besitzt. Gerade diesen auffallended Character aber teilt sie mit Lophotaspis; bin ich geneigt, *A. macdonaldi* Monticelli, trotzdem bei ihm die Genitalöffnung weiter rückwärts liegt als bei *Lophotaspis vallei,* aus dem genus Aspidogaster herauszunehmen and zu Lophotaspis zu stellen."

PARAMPHISTOMIDAE

HISTORICAL REVIEW OF THE FAMILY

The genus Amphistoma was created by Rudolphi (1801) ; concerning it Stiles and Hassall (1908) state, "Rudolphi deliberately renamed a previously validly named genus, namely Strigea Abildgaard, 1790, referring clearly to this fact both in 1801a, 50-51, and 1802b, 92. He makes but one combination (*Amphistoma subclavatum*), but since Amphistoma is clearly a new name proposed for an older one (Strigea), which Rud. changed on the alleged ground that it was inappropriate, Amphistoma should be suppressed in favor of Strigea and take the same species as type."

Fischoeder (1903) stated: "In Bezug auf den Namen Amphistomum will ich jedoch, wie schon gesehen (1901), nochmals darauf hinweisen, dass der Name Amphistoma von Rudolphi (1801) als neue Bezeichnung für die Gattung Strigea Abildg. 1790 eingeführtworden ist. Der Name Amphistoma kommt daher nach dem Prioritätsgesetz als synonym zu Strigea in Fortfall. Die ursprüngliche einzige und also auch typische Art der Gattung Strigea Abildg. 1790 (Amphistoma Rud. 1801) war *Planaria strigis* Goeze 1782 *Amphistoma macrocephalum* Rud. 1809 *Holostomum macrocephalum* Nitsch. 1819). Wenn daher der Name Strigea wieder zu Geltung wieder bebracht werden soll, so darf er nur für die heutige Gattung Holostomum weitergeführt werden, während die heutige Gattung Amphistomum einen anderen Namen erhalten muss. Ich habe in: Zool. Anz. 1900, V. 24, p. 367 den Namen Paramphistomum vorgeschlagen und, die Eintheilung nach dem Fehlen oder Vorhandensein der Pharyngealtaschen beibehaltend, in der Fam. Paramphistomidae Fischdr. (Amphistomidae Montic. 1888) die Unterfamilien Paramphistominae und Cladorchinae Fischdr. unterschieden. In diesen beiden Unterfamilien lassen sich die bekannten Formen unterbringen." The names Paramphistomum and Paraphistomidae have been accepted by Lühe, Looss, Odhner, and other writers and are used in this paper.

The paramphistomes of mammals were the first forms of this family discovered, and they have been the subjects of extensive study by Fischoeder (1903) and Stiles and Goldberger (1910) ; a number of species are known.

I have been unable to find any record of work done on the paramphistomes of fish between that of Diesing (1836) and MacCallum (1905). Daday (1907) described two species of Diplodiscus, two species of a new genus he called Microrchis, three species of a new genus named Pseudocladorchis, and added *Amphistoma oxycephalus* Dies. with two new species to the genus Chiorchis. He included a section on the anatomy and histology of the forms.

The only paramphistomes from amphibians are four species of Diplodiscus reported from frogs: *D. subclavatus* from the frogs of Europe, *D. temperatus* from those of North America, and *D. megalochrus* and *D. microchrus* from Australian frogs.

Information concerning paramphistomes of reptiles is very scanty. Braun (1901) lists three species from turtles: *Amphistoma grande* Diesing, *A. scleroporum* Creplin, and *A. sp.* Bellingham. Bellingham (1844) listed *Amphistoma sp.* from the intestine of *Chelonia imbricata* but gives no description, so this species should receive no further consideration. Braun (1901) supplemented the description of Creplin (1844) by a brief report of the single specimen of *A. scleroporum* from the museum at Greifswald, but the worm was sexually immature and consequently the observations were limited. *A. grande* was collected by Natterer from the intestine of five species of turtles in Brazil, but the description of Diesing is confined to the external appearance and the material may have comprised more than one species. One other species is known from turtles, a form described by Looss (1902) as *A. spinulosum* from the intestine of *Chelone mydas.* The description of Looss is very complete but because of the scarcity of known species and our limited knowledge of the group, at that time he refrained from any attempt at classification. He stated that the species is probably closely related to *A. scleroporum* and *A. grande.*

In addition to the description of the species, Looss (1902) discussed the question of the oral sucker and the pharynx in the group and compiling evidence from comparative anatomy and embryology, he argued that the anterior sucker of the amphistomes should be regarded as homologus to the oral sucker of the distomes. In this paper also he described the muscular thickening at the caudal end of the esophagus as a pharynx and described a peristaltic contraction of the organ from the anterior to the posterior end, altho in an earlier paper (1896) he had stated that the esophageal thickening of Gastrodiscus was not a true muscular pharynx. Concerning this latter structure, Odhner (1911) says, "Ich verwende diese Bezeichnung, weil es mir doch nicht so ganz sicher erscheint, dass es sich hier um ein dem gewöhnlichen Distomenpharynx homologes Organ handelt. Auch wenn es so wäre, könnte übrigens der ziemlich verschiedene Bau einen besondern Namen rechtfertigen; der Oesophagus müsste aber dann konsequenterweise als Präpharynx bezeichnet werden.'' In his later paper Looss (1912) referred to this organ as an esophageal bulb.

The arrangement of the fibers in concentric lamellae and the function of the organ, acting as sphincter instead of a dilating pumping organ, argue against its homology with the pharynx of the distomes. These conditions I found myself in the two species of the new genus Alassostoma. However in the other of my new forms, *Zygocotyle ceratosa*, in stead of concentric muscle lamellae, the fibers at the sides of the lumen extend radially. A thickening of the esophageal musculature is described for Gastrodiscus, Homalogaster, Diplodiscus, Microrchis, Chiorchis, Schizamphistoma, Alassostoma, and Zygocotyle. In agreement with Looss (1912), the writer regards the tube leading from the oral sucker to the intestine at the esophagus and the muscular thickening of the wall of the esophagus as an esophageal bulb.

In this same paper Looss (1912) reinvestigated the species *Amphistoma scleroporum* and described its structure in detail. Discussing the taxonomy of the species he says, ''Die Frage nach den Verwandtschaftlichen Bezeichnungen des *Amp. scleroporum* ist insofern leicht beantwortet, als seine enge Verwandtschaft zu *A. spinulosum*, auf die ich schon früher vermutungsweise hinwies (1902b, p. 437) jetzt offen zutage tritt. Ich würde nicht zögern, beide Arten in dieselbe Gattung einzureihen, wenn nicht gewisse, wenn auch kleine Differenzen im anatomischen Baue existierten die meiner Auffassung nach innerhalb von wirklich natürlichen Gattungen nicht vorkommen. Diese Differenzen bestehen, 1. in dem Fehlen des vor dem Mundsaugnapfe gelegenden starken Sphincters von *A. scleroporum* bei *A. spinulosum;* 2. der Reduction der Saugnapftaschen, die bei *A. spinulosum* deutlich, bei *A. scleroporum* nicht nach aussen hervortreten; 3. dem Fehlen der kleinen Seitenzweige an den vordersten Enden der Blasenschenkel von *A. scleroporum* bei *A. spinulosum;* 4. in dem etwas abweichenden Bau der Dotterstöcke (bei *A. scleroporum* in der Mitte fast zusammen and ohne eigentliche quere Dottergänge, bei *A. spinulosum* rein seitlich mit langen queren Dottergängen); 5. in dem etwas verschiedenen Verhalten der Lymphschläuche (ungemein reiche Verzweigung im Umkreise der Saugnäpfe bei *A. scleroporum*, kaum angedeutete Verzweigung bei *A. spinulosum*). Bin ich demnach auf Grunde dieser Unterschiede auch überzeugt, dass in den beiden Arten Repräsentanten je eines besondern Genus vorliegen, so genügt für meinen gegenwartigen Zweck doch die formelle Aufstellung der Gattung Schizamphistomum für *A. scleroporum*, in die ich *A. spinulosum* vorläufig provisorisch einbeziehe. Als die wesentlichen Charaktere dieser Gattung oder der Unterfamilie, zu der sie sich früher oder später auswachsen wird, betrachtet ich den Aufbau der Excretionblase aus zwei sehr langen, bis ins Kopfende einfachen, unter sich nicht verbundenen Schenkeln und den Aufbau des Lymphgefässsystemes aus jederseits drei in der Umgebung der Saugnäpfe verästelten Schläuchen."

He might well have added to his list of differences that in *S. spinulosum* there is a single loop of the excretory vesicle wound dorsally over the cecum of each side while in *S. scleroporum* there are eight loops winding irregularly around the cecum of each side. In the same article (p. 355) speaking of the excretory system in paramphistomes of mammals he says this system is situated deep in the body and in the larger groups is a stable and conservative organsystem. In a former paper Looss (1902 : 837) says, "Zwischen der Species einer natürlichen Gattung bestehen anatomische Unterschiede nicht; die Speciescharaktere werden dargestellt allein durch Differenzen in der Grösse des Körpers und der einzelnen Organe, Hand in Hand mit denen leichte Veränderungen ihrer Form, ihrer Lage und wenn sie reicher gegliedert oder in eine Anzahl von Theilstücken zerfallen sind, Aenderungen in der Zahl der Glieder resp. der Theilstücke gehen können." As a matter of fact, the argument of Looss in my opinion appears to show clearly that *S. scleroporum* and *S. spinulosum* are not members of the same genus; as indeed he has already suggested himself that in future researches a new genus will have to be created to contain *S. spinulosum.*

The single paramphistome reported from snakes was described by Cohn (1903) as *Amphistomum dolichocotyle*, and in his (1904) classification of the Diplodiscinae placed in the genus Catadiscus. It is from the intestine of *Herpetodryas fuscus.*

The only paramphistomes previously known from North America are *Amphistoma grande,* reported by Leidy (1888) from the intestine of the terrapin; two specimens from the small intestine of the muskrat which according to the same author, "appear to belong to *Amphistoma subtriquetrum"; Diplodiscus temperatus* Stafford long considered identical with *D. subclavatus* Dies.; and *Wardius zibethicus* Barker and East, from the cecum of *Fiber zibethicus.* The reports of Leidy contain no description except the length of the worms. Barker and East suspect that Leidy's specimens from the muskrat belong to their new genus and species *Wardius zibethicus;* and it is not unlikely that the specimens from the terrapin are specifically identical with those described here as *Alassostoma magnum* Stunkard 1916. Neither the description of Stafford nor that of Barker and East contains complete anatomical information. Stafford distinguished between the lymph and excretory systems. Barker and East make no mention of the lymph system; they state that the oral sucker is wanting and describe the anterior sucker as the pharynx, notwithstanding the arguments of Pratt (1900), Looss (1902) and Stiles and Goldberger (1910) that the anterior sucker of the amphistomes is homologous with the oral sucker of the distomes.

The material of this family available for the present study consisted of representatives of two species from North American turtles, and another species from the duck, *Anas platyrhynchos.* A study of the literature showed that these forms could not be included in any previously described genera.

THE GENUS ALASSOSTOMA

A new genus Alassostoma is formed to include the two species from turtles. The genus is characterized by the presence of large oral evaginations which open independently into the oral sucker, an esophageal bulb composed of concentric muscle lamellae, a hermaphroditic duct, germ glands near the middle of the body in the median line, both testes anterior to the ovary, vitellaria consisting of small scattered follicles in the lateral, and posteriorly in median areas of the body, Laurer's canal opening in the mid-dorsal line anterior to the opening of the excretory vesicle. *Alassostoma magnum* is to be taken as type of the genus, and in it is included also the new species *A. parvum.*

The genus Alassostoma has the type of lymph and excretory systems present in the genus Schizamphistoma and designated by Looss as characteristic of the subfamily to which that genus belongs. Looss (1912) predicted that with the discovery of other forms it would be necessary to create a new subfamily to contain them, and at that time stated the subfamily characters. With the discovery of a second genus, so similar to Schizamphistoma that the two must be included in the same subfamily, the formal recognition of the new subfamily is necessary. Schizamphistoma Looss was designated as type and the name of the subfamily becomes Schizamphistominae. The subfamily contains the genera Schizamphistoma, including also *S. spinulosum* which as already indicated by Looss and discussed in this paper is type of a new genus, and the genus Alassostoma. The distinguishing characters of the subfamily as stated by Looss are two long excretory vesicles which extend singly to the anterior end of the body and a lymph system composed of three canals on either side of the body which run longitudinally and break up into many sinuses in the regions of the suckers.

Comparisons.—When one compares the species *A. magnum* and *A. parvum* with descriptions in the literature, they are seen to agree most closely with *Schizamphistomum scleroporum* and *S. spinulosum* Looss.

Mention has previously been made of the anatomical differences existing between these species and a statement ventured that such wide and fundamental differences should not be present in a natural genus. *A. magnum* agrees with *S. scleroporum* in general appearance and size, in type of excretory and lymph systems, character of vitellaria, and in general type of reproductive and alimentary organs; but *A. magnum* has large oral evaginations, which pockets are reduced and do not extend outside the sucker in *S. scleroporum,* and *A. magnum* lacks the preoral sphincter which is present in *S. scleroporum.* In *A. magnum* the uterus and cirrus sac open to the surface thru a common hermaphroditic duct; in *S. scleroporum* they open separately. Looss (1899 : 551) says one of the most important of generic characters is the structure of the copulatory organs. In *A. magnum* the testes are further posteriad and the ovary is situated one-fourth to one-third of the body length from the posterior end instead of at the level of the anterior margin of the acetabulum as is the case in *S. scleroporum.* In *S. scleroporum* the testes and ovary are widely separated and in *A. magnum* they are comparatively close together. These differences appear to be of sufficient importance to exclude the American species from the genus Schizamphistoma.

A. magnum agrees with *S. spinulosum* in the presence of oral evaginations and lack of preoral sphincter, but differs from it in the manner of the coiling of the excretory vesicles, in the presence of a common hermaphroditic duct and in the character of the vitellaria, as well as the relative positions of the testes and ovary. The morphological facts show differences too fundamental to permit the inclusion of both these species in a single genus.

Alassostoma parvum agrees with *A. magnum* in general morphological features, presence of oral evaginations,, lack of preoral sphincter, type of lymph and secretory systems, character of genital organs and ducts, also in relative position of testes and ovary. *A. parvum* therefore agrees with and differs from *S. scleroporum* and *S. spinulosum* in the same manner as *A. magnum.* That the two forms are not different developmental stages of the same species is shown by the great difference in the size of the worms and the relative differences in the size of suckers and genital organs. One of the species of *A. magnum* 10 mm. long is not sexually mature, while in the sectioned specimen of *A. parvum* which is less that 3 mm. long spermatoza were present in the testes and vas deferens. Further, ova were present in the oviduct, and the ootype and anterior part of the uterus were filled with spermatoza. Eggs were present in only one of the seven specimens of *A. magnum* and the absence of eggs in the three specimens of *A. parvum* does not signify that it is a young stage of *A. magnum.* *A. magnum* is large and has small suckers and *A. parvum* is small and has relatively large suckers, and this feature suggested the name Alassostoma.

ALASSOSTOMA MAGNUM Stunkard 1916

[Figures 59 to 65]

The material of this species consists of one worm from *Pseudemys troosti* from Havana, Illinois; one from *P. elegans* from the same locality; two from *P. elegans* from Chicago, Illinois; and three specimens from an unknown turtle from Marshall, Missouri. The first four specimens were collected by the writer from the large intestine near its juncture with the small intestine, and the material from Marshall, Mo.,bears the label, ''From cloaca of turtle.''

In the preserved state the worms are 10 to 12 mm. in length, 3 to 5 mm. in breadth, and 1.5 to 2 mm. in thickness. One specimen studied in the living condition, measured 18 mm. in length when fully extended; preserved it is 11 mm. long, 3.8 mm. wide and 2 mm. thick. One fixed specimen 10 mm. long and 3 mm. wide is not sexually mature.

In the living state the worms are clear, hyaline, with the digestive ceca visible as brown lines. Their movements are very slow. In shape (Fig. 59) they are more or less oval, with the acetabulum forming a slight caudal projection. The acetabulum is slightly sub-terminal, circular or ovoid, usually wider near the anterior than the posterior end. The opening is necessarily relatively narrower than the sucker itself, in one specimen the opening is merely a slit, 1.4 mm. long, 0.38 mm. wide near the anterior end and posteriorly tapering to a point. In the largest specimens the acetabulum is 2.5 mm. long by 2 mm. wide, and in the smallest it is 2 mm. by 2 mm.

The cuticular covering of the body is unarmed, and measures 10 to 12μ in thickness. It is turned in at the openings of the excretory and reproductive systems and lines the digestive tract to the bifurcation. The dermo-muscular wall has the circular, longitudinal, and oblique layers well developed and inside the oblique layer there is an additional layer of longitudinal fibers (Fig. 60). Dorso-ventral fibers are scanty or lacking and the parenchyma of the body is very loose and vacuolated (Fig. 64).

Alimentary tract.—The oral sucker is terminal, spherical to ovoid in shape, usually longer in the antero-posterior axis and somewhat wider anteriorly than posteriorly. It is deeply set in the parenchyma of the body and measures 0.9 to 1.35 mm. in length and 0.6 to 0.9 mm. in width. Radial fibers pass from the external limiting membrane to the cuticula lining the sucker; in a cross section thru the sucker (Fig. 65), the inside two-thirds of the outer half is a nuclear zone and all the nuclei are collected in this area. Half way between the nuclear zone and the lumen there is a narrow band of circular fibers. The oral evaginations arise at the caudal end of the oral sucker by two separate openings, one on either side, and extend dorsad and caudad. They are 0.35 to 0.6 mm. long, flattened dorso-ventrally, 0.15 to 0.2 mm. in width. These sacs are lined with cuticula and their wall is continuous with that of the oral sucker. Externally there is a layer of longitudinal fibers and inside this sets of annular fibers (Fig. 63). Oblique and radial fibers are occasionally seen but are very scanty.

The esophagus is 0.6 to 1.3 mm. in length; it is lined with cuticula and the wall contains external longitudinal and internal annular fibers. At the caudal end of the esophagus, just anterior to the bifurcation of the alimentary tract, there is a prominent esophageal bulb. It varies from 0.65 to 0.95 mm. in length and from 0.33 to 0.5 mm. in width; it is formed by a thickening of the annular fibers of the wall of the esophagus. A cross section is represented in Figure 60 and shows the eighteen concentric lamellae of muscles. No nuclei are present in these annular muscles. Both the oral evaginations and the esophagus are surrounded by clusters of deeply staining cells (Fig. 63). Looss (1896) described similar cells in Gastrodiscus and believed they secrete the lining of the esophagus. The ceca are flattened laterally and are of very unequal caliber, small lateral evaginations occur on opposite sides at the same level recalling the condition in some of the Turbellaria. The diverticula extend almost to the acetablum, about 0.37 mm. intervening. They have a muscular coat consisting of external annular and internal longitudinal fibers and an epithelial lining of columnar cells which show faint longitudinal striations (Fig. 62).

Male Reproductive Organs.—The testes are slightly lobed, oval, longer in the transverse diameter, and vary in size from 0.27 by 0.35 mm. to 0.45 by 0.9 mm. They are situated one behind the other or in contracted specimens slightly on opposite sides of the median line. They are approximately the same size in any one specimen and are separated by about the length of one of the testes, tho in contracted specimens they may lie closer together. The vasa efferentia arise from the dorsal anterior margins, the duct from the posterior testis on the left and the duct from the anterior testis on the right side of the body. They pass dorsad and cephalad, and 0.4 to 0.5 mm. caudad of the bifurcation of the digestive tract they unite to form a much coiled seminal vesicle, which near the pore passes into a small, poorly developed cirrus sac. In sectioned individuals it could be seen that the seminal vesicle was filled with spermatoza. In one specimen the coils of the vesicle extend thru twenty cross sections each 15μ in thickness, and the tube is so coiled that in a section of the worm there are ten or fifteen sections of the vesicle. In another individual cut in frontal sections the seminal vesicle extends anteroposteriorly thru 0.57 mm. The prostate gland is enclosed by the cirrus sac and fills the entire region between the wall and the central canal. The cells are more numerous in the posterior part of the sac, gradually becoming fewer in the anterior region. The sac is approximately 0.37 mm. long and 0.185 mm. in diameter. It is dorsal on the right side of the body, and the terminal end of the uterus is ventral on the left side of the body.

Female Reproductive Organs.—The ovary is spherical or oval, 0.275 to 0.35 mm. in length and 0.33 to 0.57 mm. in width, in or near the median line, about the width of the caudal testis behind the latter. The oviduct is very small and arises from the dorsal margin of the ovary (Fig. 61). After a coil posteriad Laurer's canal is given off and passes in a winding course to the dorsal surface. There is no receptaculum seminis. Just after the origin of Laurer's canal, the oviduct passes into Mehlis' gland, where the vitelline duct is received. There is no vitelline receptacle in either of the sectioned worms, but the right and left ducts are very large. They meet in the median line posterior and ventral to Mehlis' gland, and a duct passes to the ootype. The uterus coils anteriad, either between or around the testes and opens thru the hermaphroditic duct to the genital pore.

The genital pore is in the median line ventral to the esophageal bulb, and there is a small genital sinus. The cirrus sac and metratermal portion of the uterus open to the exterior thru a common hermaphroditic duct (Fig. 60).

The vitellaria consist of small irregularly shaped follicles, lying almost entirely in the ventral half of the body and extending from the region of the cephalic testis to the caudal ends of the ceca. Anteriorly they are extraceeal, but posteriorly they extend into the intraceeal area; near the ends of the ceca about half of the follicles are between the diverticula.

Eggs were present in only one specimen. Here there were three; they measured 0.1 by 0.13 mm.

Lymph System.—This system consists of three canals passing longitudinally on either side of the body, one lateral and two mesal of each cecum. Of the median pair, one is dorsal and the other ventral (Fig. 59). These canals are not straight but wind about and give off branches at various points. These branches subdivide in turn and at the ends the main trunk breaks up into numerous smaller branches so that the entire body is penetrated by ramifications of this system. The ceca, the genital organs, and the suckers are especially well supplied with lymph sinuses.

Excretory System.—The excretory pore is in the median line on the dorsal surface, near the posterior end of the body, and the median terminal vesicle extends internally and anteriorly. It gives off a branch to either side and these branches of the collecting vesicle pass anteriad, winding about the cecum of either side in many loops or coils. In sections (Fig. 64) the tube may appear on either side, above, or below the cecum; in a single section it may be cut in two or three places or a loop may pass half to two-thirds of the way around the cecum. No connections between the collecting ducts of the two sides could be seen, and they were traced to the region of the oral sucker.

ALASSOSTOMA PARVUM Stunkard 1916

[Figures 66 to 71]

Three individuals of this species were collected from the cloaca of a single specimen of *Chelydra serpentina* from Urbana, Illinois. One was retained as an alcoholic specimen, one was stained and mounted as a toto preparation, and the third was cut into cross sections.

The worms (Fig. 66) are thick with almost parallel sides, rounded at the posterior end and tapering slightly anteriorly. Just in front of the acetabulum the body narrows slightly and then widens posteriorly due to the presence of two lateral prominences or evaginations, one on either side at the level of the anterior part of the acetabulum. The worms are 2.8 to 3 mm. long and 0.78 to 0.08 mm. wide, the points of greatest width are at the level of the testes and thru the posterior lateral prominences. The sectioned worm is 0.8 mm. in width and 0.54 mm. in thickness. The acetabulum is subterminal, oval, 0.8 mm. in length and 0.7 mm. in width in the toto preparation. The inside measurements of the same sucker are 0.56 mm. in length by 0.4 mm. in width and the opening is 0.45 mm. in length and 0.21 mm. in greatest width.

Alimentary Tract.—The oral sucker is terminal, ovoid, 0.46 mm. long by 0.37 mm. wide, and in the sectioned worm 0.32 mm. in depth. In the mounted specimen the sucker is widest posteriorly, and from the posterior dorsal part on either side there is an oral evagination. These arise separately and are 0.055 mm. long. Among the fibers of the oral sucker there are many nuclei; they are situated in the peripheral half of the sucker and are confined to the central two-thirds of the external half. There are also among the muscle fibers glandular cells with ducts to the lumen of the sucker. The esophagus is somewhat coiled but extends thru 0.2 mm. and is surrounded by large deeply staining gland cells. The posterior part is enlarged by the thickening of the annular muscles of the wall which forms the esophageal bulb (Fig. 70). This structure comprises twelve concentric rings or lamellae of muscles. It is 0.2 mm. long by 0.14 mm. wide in the toto specimen and 0.314 mm. in depth in the sectioned individual. The diverticula extend posteriad almost to the cephalic margin of the acetabulum. In sections they are oval, and flattened laterally. In the intestine of the sectioned worm there are masses of small nuclei, possibly from the epithelial lining of the cloaca of the host.

Male Reproductive Organs.—The testes are oval, in the toto specimen they are 0.17 mm. long by 0.17 mm. wide, and in the sectioned worm 0.17 mm. wide by 0.29 mm. thick. They are situated one in front of the other in the median line and in the ventral part of the body. They are close together, separated only by a thin fibrous sheet. The vasa efferentia arise at the dorsal margins of the testes; the duct from the caudal testis pass anteriad and anterior to the cephalic testis unites with the duct from this latter testis. The vas deferens immediately expands into a long much-coiled seminal vesicle which passes anteriad and into the cirrus sac (Fig. 69). Inside the cirrus sac the tube continues in large coils; the terminal part is surrounded by the cells of the prostate gland and opens to the surface thru a short hermaphroditic duct. There is a small genital papilla (Fig. 71).

Female Reproductive Organs.—The ovary is oval; in the toto specimen it is 0.098 mm. long and 0.088 mm. wide, and in the sectioned worm it is 0.95 mm. wide and 0.134 mm. thick. It is median in position and situated midway between anterior and posterior ends of the body. The oviduct arises at the dorsal posterior margin and passes dorsad and posteriad into Mehlis' gland. This gland is large and well developed. Here Laurer's canal is given off and passes in short coils to the dorsal surface. Just after the origin of Laurer's canal a short common vitelline duct opens into the ootype and the oviduct passes ventrad. It expands to form the initial part of the uterus, turns anteriad, and is filled with masses of spermatoza. The expanded portion of the uterus extends anteriad half the distance to the caudal testis and then the tube contracts, passes dorsad and in a winding course over the testes. Anterior to the testes it turns ventrad and enters the hermaphroditic duct on the posterior ventral side. The vitellaria extend from the region of the testes to the caudal ends of the digestive ceca and consist of scattered lobes, mostly ventral in position. Anteriorly they are extracecal but behind the ovary they are intracecal as well.

No eggs were present in any of the specimens.

The genital pore is in the midventral line, just posteror to the bifurcation of the alimentary tract. There is a genital sinus but no genital sucker.

Lymph System.—The lymph system is similar to that described for *A. magnum* and consists of the three longitudinal canals on either side of the body, one canal lateral to each cecum and a pair, one dorsal and the other ventral, mesal to the diverticulum of either side. The secondary branchings could not be traced but lymph sinuses are present in sections in all parts of the body, and those around the acetabulum are shown in Figure 68.

Excretory System.—The excretory pore is median, dorsal, at the level of the cephalic margin of the acetabulum. A short median vesicle passes ventrad and anteriad and divides into two collecting vesicles as in *A. magnum.* These pass ventrad and posteriad, one on either side, loop around the caudal ends of the diverticula, and then turn anteriad, winding around the ceca in many irregular coils so that in sections they appear lateral, mesal, ventral or dorsal to the intestine; often the tube is cut two or three times in the same section or a single section may show a coil encircling the cecum for half or more of its circumference (Fig. 67). Anterior to the bifurcation of the alimentary tract the ducts continue in the lateral areas of the body and can be traced almost to the oral sucker.

THE GENUS ZYGOCOTYLE

The only known form with which the paramphistomes from the duck can be compared is *Amphistoma lunatum.* This species was described by Diesing (1836) ; the material had been collected by Natterer in Brazil, South America, from the cecum of *Anas melanotus, A. ipecutiri, A. moschata, Himantopus wilsonii,* and also from the cecum of *Cervus dichotomus.* Fishoeder secured the original specimens from the Vienna museum and (1903) gave a more extended description of the form, altho his study was restricted to the examination of toto preparations. He stated that the citation of *Cervus dichotomus* as a host of this form is probably an error, and the same suspicion had been mentioned by Diesing (1850). It is at once apparent that the present species is very similar to *A. lunatum.* Both are parasites of American ducks, and are the only paramphistomes at present known from avian hosts. They are nearly equal in size, are similar in shape, have a subterminal oral sucker, reproductive systems that compare very closely, digestive tracts similar in character, and acetabula of the same form consisting of an anterior section and a posterior overhanging lip which terminates on either side in a small cone-like projection.

Amphistoma lunatum has been placed as an appendix to every classification of the paramphistomes that has ever been attempted. With the discovery of a form so similar, the two must belong together and a new genus is proposed to contain the two species. The peculiar divided condition of the acetabulum suggested the name Zygocotyle as appropriate for this genus. *Zygocotyle ceratosa* has been designated as type and in the genus is included also the species *Amphistoma lunatum*.

As diagnostic characters of the genus Zygocotyle may be mentioned the subterminal oral sucker, the posterior sucker divided or provided with caudal overhanging lip, absence of cirrus sac and separate openings of the male and female ducts. Others will undoubtedly appear when the character of the excretory and lymph systems are known. The genus Zygocotyle differs from all other known genera of the Paramphistomidae in the ventral position of the oral sucker and the peculiar character of the acetabulum. It differs from the Gastrodiscinae in the shape of body and absence of ventral papillae, and from the Gastrothylacinae in the absence of the ventral pouch. In the lobed testes and absence of cirrus sac it agrees with the Paramphistominae, but the oral evaginations exclude it from that group. The absence of cirrus sac and the lobed form of the testes will not permit its inclusion with the Cladorchinae. The characters of the Diplodiscinae are so poorly defined that a comparison is unsatisfactory; in this group however, a cirrus sac is present and both suckers are terminal. As none of the existing subfamilies will include the genus, a new subfamily will probably have to be made to contain it. Since the present classification of the Paramphistomidae is somewhat uncertain, and the structure of the excretory and lymph systems of this genus are as yet unknown, no further attempt at classification of the group is made at this time.

ZYGOCOTYLE CERATOSA Stunkard 1916

[Figures 72 to 79]

The material of this species consists of eight specimens from the intestine of *Anas platyrhynchos* from Rock County, Nebraska. The intestine of the duck had been cut open in places and together with its contents preserved in formalin. The fixation of the parasites is so poor that the excretory and lymph system can not be traced, altho remnants of both appear in sections.

These worms (Fig. 72) vary in length from 3 to 6 mm. and in width from 1.45 to 2.14 mm. In dorsal or ventral aspect they are elongate oval in shape with the acetabulum forming a small terminal projection. The cross section is a flattened oval and toward the ends of the body becomes more circular. The acetabulum is subterminal and consists of two parts (Fig. 77), an anterior part extending dorsally and anteriorly into the body and a posterior overhanging lip which terminates on either side in a little horn or conical projection 0.12 to 0.2 mm. in length. The cephalic part extends anteriad about 0.46 mm. from the anterior margin of the opening of the sucker. The opening of the acetabulum is oval approximately 1.1 mm. in length and 0.74 mm. in diameter. The septum or partition which divides the sucker extends almost to the opening and appears to separate an anterior circular part from the remaining portion but there is a single oval opening of the acetabulum.

The cuticula is unarmed, slightly thicker on the dorsal surface. On the ventral surface it is about 12μ in thickness and reaches 30μ in thickness on the dorsal surface. It is not homogeneous, but is traversed by fine crinkled lines extending from internal to external surfaces, which give it a reticulated appearance. The entire dorsal surface of the body is underlaid with large gland cells filled with a substance staining deeply with haematoxylin; and their ducts lead to the dorsal surface. The contents of the gland cells and their ducts have the same appearance and staining reaction as the cuticula of the external surface. The dermomuscular sac consists of the usual circular, longitudinal, and oblique layers, the circular layer is next to the cuticula. From the body wall there are many large dorso-ventral muscle strands extending thru the body.

Alimentary Tract.—The oral sucker is subterminal, circular or slightly oval in shape, 0.37 to 0.53 mm. in diameter. The oral evaginations are 0.15 to 0.22 mm. in length and 0.07 to 0.1 mm. broad; they branch one on either side from a common sinus (Fig. 74) which opens into the dorsal side of the posterior part of the oral sucker. The esophagus leads from the oral sucker to the intestine; it is 0.05 to 0.37 mm. in length and is surrounded by a layer of deeply staining cells. Its caudal portion is surrounded by an esophageal bulb. This structure is oval, 0.2 to 0.45 mm. in length, 0.18 to 0.23 mm. in width, and 0.35 mm. in thickness in the specimen cut in cross sections. It is situated obliquely in the body, the anterior end is ventral and the posterior end more dorsal in position. The muscles are not arranged in concentric lamellae as in the previously described paramphistomes; there is a capsule of external longitudinal fibers and the body of the organ is composed of fibers extending on the sides from the central canal to the external capsule and above and below the canal the fibers extend across from the lateral walls of the bulb (Fig. 73). The alimentary tract is lined with cuticula to the bifurcation. The ceca are flattened laterally and the lateral walls are sinuous giving them a very irregular appearance. They have a muscular wall composed of outer circular and inner longitudinal fibers and extend almost to the opening of the acetabulum, about 0.1 to 0.15 mm. intervening. They terminate just caudad of the excretory pore.

Male Reproductive Organs.—The testes lie one behind the other in the median line, the caudal testis is almost in the center of the body, and the cephalic testis is about 0.2 mm. in front of it. They are about the same size, lobulated, oval, crosswise of the body, almost touching the cecum of either side. They are ventral in position, almost touching the ventral body wall and not extending far into the dorsal half of the worm. They vary in size from 0.2 by 0.3 mm. in the smallest to 0.55 by 0.78 mm. in the largest specimen. The vasa efferentia arise from the anterior dorsal margins, the right tube from the anterior and the left tube from the posterior testis. Near the genital pore they unite and form a much coiled seminal vesicle which has a thickened muscular wall. This structure extends thru twenty-five cross sections cut 10μ thick. The terminal part that leads ventrad to the genital pore is expanded, the walls are thinner, and this part is surrounded by the cells of prostate gland. A cirrus sac is absent, the male and female tubes open to the exterior independently at the apex of a slight ventral prominence. The opening of the male duct is immediately anterior to that of the female (Fig. 78).

Female Reproductive Organs.—The ovary is oval, lobulated, crosswise of the body, about the shorter diameter of the testis behind that organ. In the smallest specimens it is 0.2 by 0.33 mm. and in the largest 0.33 by 0.52 mm. The oviduct arises at the dorsal margin as a very small tube and passes dorsad where Laurer's canal is given off. This canal winds in short curves to the dorsal surface, opening anterior to the excretory pore (Fig. 79). After the origin of Laurer's canal the oviduct passes posteriad and ventrad into Mehlis' gland where a short common vitelline duct is received. The uterus then coils irregularly in close folds to the genital pore. The uterine coils are largely in the dorsal part of the worm altho they may extend into the ventral portion and coil around the testes. Laterally the coils of the uterus are limited by the ceca. The terminal part has a slight thickening of the wall but not a distinct delimited metraterm. The vitellaria are well developed, large follicles extending in the extracecal areas from the level of the posterior edge of the oral sucker to the anterior margin of the opening of the acetabulum. They are limited medially by the ceca and laterally extend almost to the body wall. They are more ventral than dorsal in position.

Eggs are present in large numbers. In size they average 0.14 by 0.083 mm.

Comparison.—*Zygocotyle ceratosa* agrees with *Z. lunata* in length, width, and size of oral sucker, but in the former species the oral evaginations are smaller, the esophagus is much shorter, the testes and ovary are oval and lobed instead of circular, and the ceca do not extend to the opening of the acetabulum. In *Z. ceratosa* the acetabulum is nearer the ovary, and the vitellaria are entirely extracecal while in *Z. lunata* they extend between the ceca.

CLASSIFICATION OF THE FAMILY

Our present classification of the Paramphistomidae is largely the result of the work of Monticelli, Otto, Fischoeder, Cohn, Daday, Stiles and Goldberger, Looss, and Odhner.

The first division of the group was made by Monticelli (1892) when he separated Gastrodiscus from the rest and created the subfamily Gastrodiscinae. Fischoeder in a series of papers described several species from mammals, and formulated (1903) the second scheme of classification. He created two subfamilies: Paramphistominae in which the testes are lobed, and paired oral evaginations and cirrus sac are absent; and Cladorchinae characterized by branched testes and the presence of paired oral evaginations and cirrus sac. Recent additions to our knowledge of the family have, however, rendered it difficult to use these distinctions satisfactorily. Cohn (1904) created the subfamily Diplodiscinae to contain the genera Diplodiscus, Opisthodiscus, and Catadiscus. He characterized the subfamily as follows: "Amphistomiden von gedrungener, konischer Form und runden Querschnitt. Mundsaugnapf gut ausgebildet, mit zwei retrodorsal Taschen. Ein grosser Endsaugnapf, über welchem dorsal der Excretionsporus liegt. Mundöffnung terminal, Darmschenkel bis zu Endsaugnapf reichend, relativ sehr breit. Leben im Enddarm von Amphibien und Reptilien." The characterization is inadequate, since the anatomical features are shared by almost half the members of the family, and obviously further study of this group is necessary to establish its validity and determine its true diagnostic features.

Stiles and Goldberger (1910) proposed a new classification of the group. They created a new superfamily Paramphistomoidea to contain the forms previously classed as amphistomes. They removed Gastrodiscus Leuck., and Homalogaster Poir. from Fischoeder's subfamily Cladorchinae and created a new family Gastrodiscidae to contain these genera. They created another new family Gastrothylacidae to contain the general Gastrothylax, Wellmanius, Carmyerius, and Fischoederius. The family Paramphistomidae and the two cited above comprise the three families in the superfamily Paramphistomoidea. Stiles and Goldberger also created a new subfamily Stephanopharynginae to contain the genus Stephanopharynx, and added the new genus Cotylophoron to the subfamily Paramphistominae. They recognize further the subfamily Diplodiscinae Cohn and list the four subfamilies Paramphistominae, Cladorchinae, Diplodiscinae, and Stephanopharynginae in the family Paramphistomidae. They placed Balanorchis in the subfamily Cladorchinae notwithstanding Fischoeder's statement that such an arrangement could not be considered.

Braun (1911) reviewing the article, objects to the rank of superfamily for the paramphistomes and says placing them on an equality of rank with the Fascioloidea is not justifiable.

The work of Stiles and Goldberger is criticized at the hands of Odhner (1911) as follows: ''Dies alles zeigt nun evident, wie wenig Verstandnis die betreffenden Autoren für die moderne natürliche Digenensystematik haben. . . . . . Mir scheint nun diese ''Argumentation'' ebenso wie viel anders (die neue topographische Terminologie) in derselben arbeit sehr ''unwise'' zu sein. . . . . die Amphistomen entsprechen im systematischen Range einer einzelnen Distomenfamilie und nicht, wie Stiles and Goldberger gelaubt haben, der Summe sämtlicher dieser Familien.''

Looss (1912) also gives a critical review of the paper: Die Charakterisierung der Arten, Gattungen usw. baut sich auf, einerseits auf eine pedantisch ins einzelne gehende Analyse und Beschreibung der Körperform und der Topographie von Darm und Genitalapparat, anderseits auf eine konsequente Ignorierung der beiden Tatsachen, dass die Tiere, als Organismen, innerhalb gewisser Grenzen natürlich variieren, und dass Körperform sowohl wie Topographie der Organs mit dem Wachstum gesetzmässige, mit der Kontraktion a priori nicht bestimmbare Veränderungen erleiden. Der Aufbau von Lymph—und Excretionsapparat bleibt völlig unberücksichtigt. Dass die Amphistomen ein ''Lymphgefässsystem'' überhaupt besitzen, scheint den Autoren unbekannt zu sein.''

The classification of Stiles and Goldberger as pointed out by other authors is based on superficial characters and the elevation in rank of the family and groups within the family is in most cases unwarranted. However, the subfamily Gastrothylacinae of these authors appears to be clearly distinguished by the presence of the large ventral pouch, and in my opinion should be retained.

Looss (1912) considers the lymph and excretory systems of major importance in classification. As characters of the new subfamily Schizamphistominae he mentioned the type of lymph and excretory systems. Since the lymph system has not yet been described in other subfamilies, the former diagnoses based on body form, types of digestive and reproductive systems, presence of ventral pouch, etc., must be retained for the present. Moreover, since so many of the forms are incompletely described, and considerable difference of opinion exists in regard to the taxonomic value of the different features, the classification of the group is still uncertain. As Looss (1912) says, ''Jeder Klassifikationversuch, der der bau von Excretions—und Lymphgefässsystem ausser acht lässt, mag sich wohl einen Klassifikationsversuch nennen, kann aber niemals

Anspruch darauf erheben, als naturlicher oder (was dasselbe ist) wissenschaftlicher Klassifikationsversuch anerkannt zu werden.'' In the same article he states that for many years he has been engaged in preparing a revision of the amphistomes but has not yet completed the work which will present a classification based on the structure of the lymph and excretory systems and the copulatory apparatus.

The only arrangements of the genera of the family that have been made heretofore are those of Fishoeder and of Stiles and Goldberger. The classification of Fischoeder does not appear adequate and that of Stiles and Goldberger is far from satisfactory, but for sake of completeness both are appended in outline.

Classification of Fischoeder (1903)

- Paramphistomidae
  - Paramphistominae
    - Paramphistomum
    - Gastrothylax
    - Stephanopharynx
      - Species inquirendae, *A. gigantocotyle*
        A. explanatum
  - Cladorchinae
    - Cladorchis
    - Gastrodiscus
    - Homalogaster
    - Diplodiscus
    - Chiorchis
      - Species inquirendae; *A. hawkesi, A. collinsi, A. ornatum, A. papillatum, A. tuberculatum, A. emarginatum,* and *A lunatum.*
  - (Subfamily nov.)
    - Balanorchis

Classification of Stiles and Goldberger (1910)

- Paramphistomoidae
  - Gastrodiscidae
    - Gastrodiscus
    - Homalogaster
  - Gastrothylacidae
    - Gastrothylacinae
      - Gastrothylax
      - Wellmanius
      - Carmyerius
      - Fischoederius

- Paramphistomidae
  - Paramphistominae
    - Paramphistomum
    - Cotylophoron
  - Cladorchinae
    - Cladorchis
    - Taxorchis
    - Chiorchis
    - Microrchis
    - Pseudocladorchis
    - Pseudodiscus
    - Balanorchis
    - Watsonius
    - Pfenderius
  - Diplodiscinae
    - Diplodiscus
    - Catadiscus
    - Opisthodiscus
  - Stephanopharynginae
    - Stephanopharynx

As a result of my studies on this family, certain data have been added and some doubtful points cleared up. The discovery of the two species of the new genus Alassostoma and the demonstration of their position as members of a new genus in the subfamily Schizamphistominae Looss establishes that group. The description of the new genus and species *Zygocotyle ceratosa* throws considerable light on the previously isolated and obscure species *A. lunatum* Dies. In conclusion I present a tentative revision of the paramphistomes. In the main it is my interpretation of the status of the group and its subdivisions. The new genera of Stiles and Goldberger are included without comment altho certain authors do not recognize their validity. I have had no opportunity to work on this material and consequently any judgment on my part must appear unwarranted. Because of the scarcity of known forms and the incompleteness of most of the descriptions it is impossible to present a final classification. The following arrangement is provisional and likely to be replaced whenever a natural system can be formulated for the family.

- Paramphistomidae Fischoeder 1901
  - Gastrodiscinae Monticelli 1892
    - Gastrodiscus
    - Homalogaster
  - Paramphistominae Fischoeder 1901

- Paramphistomum
- Stephanopharynx
- Cotylophoron

Cladorchinae Fischoeder 1901
- Cladorchis
- Taxorchis
- Chiorchis
- Pseudodiscus
- Microrchis
- Pseudocladorchis
- Watsonius
- Pfenderius

Diplodiscinae Cohn 1904
- Diplodiscus
- Opisthodiscus
- Catadiscus

Gastrothylacinae Stiles and Goldberger 1910
- Gastrothylax
- Wellmanius
- Carmyerius
- Fischoederius

Schizamphistominae Looss 1912
- Schizamphistomum
- (*Gen. nov.*) *spinulosum*
- Alassostoma
- Genera of uncertain position

————————(new subfamily) Fischoeder 1903
- Balanorchis

————————(new subfamily) see text p. 71
- Zygocotyle

RELATION OF THE FAMILIES TO THE ORDER

The trematodes are generally regarded as descended from a turbellarian-like ancestor which possessed a posterior sucker. With the assumption of the parasitic habit adaptations began in various directions. The ectoparasitic forms retained many of their former characters while the added protection and food supply afforded those specializing toward endoparasitic existence provided for perpetuation and distribution of the species thru the excessive development of the reproductive apparatus. The development of the ectoparasitic forms is simple and direct while that of most if not all endoparasites has been complicated by the interpolation of one or even more secondary or intermediate hosts.

The differences in type of adhesive apparatus may in a general way be explained thru differences in habit. The oral sucker has developed thru continued adhesion by the anterior end in maintaining position, in locomotion, and in securing food. In the Gasterostomidae the mouth is on the ventral surface and an independent anterior sucker is developed, altho this is undoubtedly a secondary feature, as in the cercariae of these forms there is a single anterior oral sucker. In response to the constant necessity for strong adhesion the ectoparasitic species have developed accessory posterior organs of attachment, while in most of the endoparasitic forms the acetabulum has migrated anteriad or disappeared entirely.

The general classification of Monticelli, which is followed in this paper, is based primarily on the character of the adhesive apparatus. In the Heterocotylea the posterior sucker has been replaced by a disc which bears suckers and hooks; in the Aspidocotylea the acetabulum has become specialized into a multiloculate adhesive organ; and in the Malacocotylea the acetabulum may be retained in its primitive terminal position, or it may have migrated anteriorly, in certain cases being reduced and in others disappearing entirely. In the young individuals of many forms in each of the three groups there is a single posterior sucker and this fact adds weight to the theory that the present groups are descended from a primitive form with a simple posterior sucker. In the young stages of all the Aspidogastridae there is a simple posterior sucker and the worm closely resembles a young distome. In the early stages of the Heterocotylea the reversion to the ancestral conditions is not so complete, and specialization in this group shows clearly that it is widely separated from the other two suborders which thru the presence of similar young forms appear to be more closely related.

The morphological structure and direct development of the Polystomidae at once places them with the Heterocotylea. In the adoption of an endoparasitic mode of life, however, thy show a distinct departure from the other members of the suborder. The present study of the Polystomidae has emphasized the unusual morphological variation and wide geographic distribution which exists in the family. This may mean either that the family is very old and has been subjected to conditions producing wide variation, or that the group really lacks family entity and consists of various heterocotylean forms which have specialized in the direction of an endoparasitic habit and that the morphological resemblance is cenogenetic.

Pratt (1908) reviews the literature and arguments for convergent development which are based on trematode morphology. Johnston (1914) argues for divergence as the true explanation of the variation of the species of Pneumoeneces, Gorgoderinae, Brachycoelinae, etc., and believes that the elucidation of trematode phylogeny may be sought in the study of the relationships between the distribution of trematode parasites and the distribution of their hosts. No doubt the likenesses and differences in the structure of present species are the result of both convergence and divergence; yet it seems that the distributional factor emphasized by Johnston is not of major importance. Parasitic distribution could precede the distribution of the primary and secondary hosts only in case the parasites changed to new primary or secondary hosts. But today more than one species may serve as primary or secondary host; the parasite is probably in a restricted degree able to adapt its life history physiologically so other species may serve as hosts, and primitively this adaptability may have been greater than now. The distribution of the parasites certainly depends to a large extent on the distribution of the primary host, and to a less extent on the distribution of the secondary host, but the presence of two similar parasites in the same region does not prove that their hosts had primitively the same or different parasites. The life history of the trematodes is so imperfectly known that at present no final decision can be made on this basis.

The wide variation in structure of the members of the genus Polystoma can not be adequately explained thru migration, or thru differences in the age of the parasite, type of host, or location in the host. In the genus so far as is known, the long uterus containing many eggs is confined to species infesting the urinary bladder of amphibian hosts of the Old World. However in respect to other characters, e. g., the shape of the caudal disc and absence of great hooks, these amphibian forms of the Eastern hemisphere disagree with each other and agree with forms parasitic in the urinary bladder and oral cavity of North American turtles. The turtle parasites have a very similar structure, whether parasitic in the urinary bladder or in the pharyngeal cavity. Furthermore, if the observations of Zeller are correct and the individuals of *P. integerrimum* becoming mature on the gills of tadpoles lack external vaginae and have a spherical testis and a single egg in the uterus, one is entirely at a loss to explain the variation existing in the genus.

In the Aspidogastridae the young individuals have an oral sucker and a small posterior acetabulum without dividing ridges, and very closely resemble young distomes. The mode of infection is almost entirely unknown, and this offers a promising field for investigation. The discovery of the sexual form of Stichocotyle by Odhner (1898) establishes the fact that at least one species of the Aspidogastridae has an intermediate host. Nickerson (1895) observes, "Owing to the well known tendency of fresh water conditions to obliterate larval life, it may well be that Aspidogaster has secondarily lost a more or less complicated series of changes, which have been retained by its relatives inhabiting salt water." The presence within the family of both direct and indirect development, together with other characters common to both the Heterocotylea and Malacocotylea designate it as an intermediate group. The morphological structure is similar to that of the Malacocotylea while the manner of development is similar to that of the Heterocotylea. Whether the Aspidogastridae are primitive forms or are secondarily degenerate is as yet undecided. The simple and archaic character of the intestine, the eye spots, the direct development and the ectoparasitic habit as it occurs in the family, together with the parasitic infection of molluscs by adult forms strongly suggests a very primitive and ancient group. It is probable that complete evidence concerning the structure and life history of this family would go a long way toward solving the problem of whether the invertebrate or the vertebrate is the original host and the attendant problem of the origin of double hosts.

The Paramphistomidae appear to be a primitive family of the Malacocotylea that have retained the original caudal sucker, altho certain species show specializations of the organ from the simple spherical type. Considerable light is thrown on the relationships of the Malacocotylea by the recent work of Odhner on a natural system for the digenetic trematodes. He strongly advocates the view that the monostomes are a group which have no family entity, and consist of individual forms derived from various distome groups which have alike lost the acetabulum. Pointing out close and fundamental agreement in internal structure he argues that the monostome family Angiodictyidae is really a subfamily of the Paramphistomidae. He shows essential morphological agreement between *Distoma quadrangulum* Daday and the fish amphistomes. His examination of the original specimen of Aspidocotyle confirms the statement of Braun (1879-1893) that this form belongs to the amphistomes, altho its relation to the other members of the group is uncertain. Further he states that the Gasterostomidae by the structure of the cercaria as shown in the oral sucker and the presence and relations of the oral evaginations, doubtless belongs to the Paramphistomidae. His derivation of the gasterostomes thus from amphistome-like forms of frogs is plausible since the frogs serve as food for the hosts of the gasterostomes. To Odhner's argument may be added that the divided condition of the body in Gastrodiscus recalls the similar condition in certain Aspidogastridae and suggests a possible relationship between these forms. The morphological comparisons of Odhner and other writers appear to show very clearly that divergence and convergence have both had great influence on the phylogeny of certain trematode families.

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A preliminary description was given in the Journal of Parasitology, 3:21-27.

BIBLIOGRAPHY

André, J.

1910. Zur Morphologie des Nervensystems von *Polystomum integerrimum* Froel. Zeit. f. wiss. Zool., 95:191-202, 11 figs.

1910a. Die Augen von *Polystomum integerrimum* Froel. Zeit. f. wiss. Zool., 95:203-220, 13 figs.

Baer, K. E.

1827. Beiträge zur Kenntniss der niedern Thiere. Nov. act. acad. nat. cur., 13, pt. 2, pp. 524-762. (Cited after Braun 1879-93.)

Barker, F. D.

1915. Parasites of the American Muskrat. Jour. Paras., 1:184-198, 2 pl.

Barker, F. D., and Parsons, S.

1914. A New Aspidobothrid Trematode from Lesseur's Terrapin. Trans. Amer. Micr. Soc., 33:261-262.

Beauchamp, P. de

1913. *Polystomum alluaudi*, n. sp. Voy. de Ch. Alluaud et R. Jeannel, Resultats Scientific, Memoirs 1913, 3 figs.

Bellingham, O.

1844. Catalogue of Irish Entozoa, with Observations. Ann. and Mag. Nat. Hist., 13:340.

Beneden, P. J. van

1858. Mémoire sur les vers intestinaux. Compt. rend. Acad. Sci. Paris, Suppl., 2:1-376, 27 pl.

Beneden, P. J. van, et Hesse, C. E.

1863. Récherches sur les Bdellodes et les Trématodes marins. Arch. roy. Belgique, 34:1-150, 15 pl.

Benham, W. B.

1901. The Platyhelmia, Mesozoa, and Nemertini. Treatise on Zoology (Lankester), pt. 4.

Blainville, M.

1828. Vers. Dict. d. sci. nat. (Cited after Braun 1879-93.)

Brandes, G.

1892. Zum feiner Bau der Trematoden. Zeit. f. wiss. Zool., 53:558-577, pl. 22.

Braun, M.

1792. Fortsetzung der Beyträge zur Kenntnis der Eingeweidewürmer. Sch. d. Berlin Ges. nat. Frde., 10:57-65, pl. 3. (Cited after Braun 1879-93.)

Braun, M.

1879-1893. Vermes. A. Trematodes. Bronn's Klass. u. Ordnung. d. Thierreichs, Bd. 4, Aht. 1.

1901. Die Trematoden der Chelonier. Mitt. Zool. Mus. Berlin, 2:13-20, 1 pl.

1911. [Review of Stiles and Goldberger 1910.] Zool. Zent., 18:705-707.

BURMEISTER, R.

1856. Zoonomische Briefe. Allgemeine Darstellung der thierischen Organization. Leipzig, pp. 250-252.

CERFONTAINE, P.

1896. Contribution à l'étude des Octocotylidés. Arch. Biol., 14:497-552, 4 pl.

1898. Contribution à l'étude des Octocotylidés. Arch. Biol., 15:301-366, 9 figs.

DELLE CHIAJE, S.

1823-1829. Memorie sulla storia e notomia degli animali senza vertebre del regno di Napoli· 4 vol. Napoli. (Cited after Stiles and Hassall 1902-1912.)

COHN, L.

1903. Zur Kenntnis einiger Trematoden. Cent. Bakt. und Par., 34:35-42. 4 figs.

1904. Helminthologische Mitteilungen II. Arch. f. Naturg., pt. 1, 70:229:252.

CREPLIN, F. C. H.

1844. Endozoologische Beiträge. Arch. f. Naturg., 10:112-133, 1 pl.

CUNNINGHAM, J. T.

1884. A New Marine Trematode Belonging to the Polystomidae. Zool. Anz., 7:399.

1887. On *Stichocotyle nephropis,* a New Trematode. Trans. Roy. Soc. Edinb., 32:273-280, 1 pl.

DADAY, E. VON

1907. In südamerikanischen Fischen lebende Trematoden-Arten. Zool. Jahrb., Syst., 24:469-590, 6 pl.

DELAROCHE, F. E.

1811. Sur deux animaux vivant sur les branchies des poissons. N. Bull. Soc. Philom. Par., 2:270-272, pl. 2. (Cited after Stiles and Hassall, 1902-1912.)

DIESING, K. M.

1836. Monographie der Gattungen Amphistoma und Diplodiscus. Ann. Wien. Mus. Naturg., 1:235-260, 3 pl.

1850. Systema Helminthum. Vindobonne 1850. vol. 1:285-477.

1859. Nachträge und Verbesserungen zur Revision der Myzhelminthen. Sitzg. K. Ak. Wiss. Wien, math-nat. Cl., 35:421-454.

DUJARDIN, F.

1845. Histoire naturelle des helminthes ou vers intestinaux. Paris.

FISCHOEDER, F.

1901. Die Paramphistomiden der Säugethiere. Zool. Anz., 24:367-375.

1903. Die Paramphistomiden der Säugethiere. Zool. Jahrb., Syst., 17:485-660, 11 pl.

FORBES, S. A.

1896. *Cotylaspis insigne.* Bien. Rep. St. Lab. Nat. Hist. Springfield, Ill.

FRÖHLICH, J. A.

1789. Beschreibungen einiger neuer Eingeweidewürmer. Naturforscher, Halle, 24:101-162, figs. 1-31. (Cited after Stiles and Hassall, 1902-1912.)

1791. Beyträge zur Naturgeschichte der Eingeweidewürmer. Naturforscher, Halle, 25:52-113, 17 figs. (Cited after Stiles and Hassall, 1902-1912.)

GOLDSCHMIDT, R.

1902. Untersuchungen über die Eireifung, Befruchtung und Zelltheilung bei *Polystomum integerrimum* Rud. Zeit. f. wiss. Zool., 71:397-445, 3 pl.

1902a. Bemerkungen zur Entwicklungsgeschichte des *Polystomum integerrimum* Rud. Zeit. f. wiss. Zool., 72:180-189, 11 figs.

1909. Eischale, Schalendrüse und Dotterzellen der Trematoden. Zool. Anz., 34:481-498.

GOTO, S.

1894. Studies on the Ectoparasitic Trematodes of Japan. Jour. Coll. Sci., Imp. Univ. Japan, 8, pt. 1, 300 pp., 27 pl.

1899. Notes on Some Exotic Species of Ectoparasitic Trematodes. Jour. Coll. Sci., Imp. Univ. Japan, 12:263-295, 2 pl.

HALKIN, H.

1902. Recherches sur la maturation, la fécondation et la développement du *Polystomum integerrimum.* Arch. d. Biol., 18:291-359, pl. 10-14.

HASWELL, W. A.

1907. Genito-intestinal Canal in Polyclads. Zool. Anz., 31:643-644.

HOYLE, W. E.

1888. Trematoda. Encyc. Brit. 9 ed., 23:535-540.

IJIMA, I.

1884. Ueber den Zusammenhang des Eileiters mit dem Verdauungscanal bei gewissen Polystomeen. Zool. Anz., 7:635-639.

JÄGERSKIÖLD, L. A.

1899. Ueber den Bau von *Macraspis elegans.* Öfvers. Vet-Akad. Fordh., 3:197-214, 1 pl.

JOHNSTON, S. J.

1912. On Some Trematode Parasites of Australian Frogs. Proc. Linn. Soc. N. S. Wales, 37:285-362, pl. 14-43.

1914. Trematode Parasites and the Relationships and Distribution of their Hosts. Rep. Austral. Ass. Adv. Sci., 1914:272-278.

KELLY, H. M.

1899. A Statistical Study of the Parasites of the Unionidae. Bull. Ill. St. Lab. Nat. Hist., 5:399-418.

KOFOID, C. A.

1899. On the Specific Identity of *Cotylaspis insignis* Leidy and *Platyaspis anadontae* Osborn. Zool. Bull. Boston, 2:179-186.

KUHL, H., und HASSELT, J. C. VAN

1822. *Polystoma midae.* Isis, 1822:113-115. (Cited after Braun, 1879-1893.)

KUHN, J.

1829. Description d'un nouvel epizoaire du genre Polystomum qui se trouve sur les branchies de la petite roussette (*Squalus catulus*) suivie de quelques observations sur le *Distomum megastomum leporis.* Ann. d. sc. d'obs., 2:460-465.

LEIDY, J.

1851. Helminthological Contributions II. Proc. Acad. Nat. Sci. Phila., 5:224-227.

1857. Observations on Entozoa Found in the Naiades. Proc. Acad. Nat. Sci. Phila., 9:18.

1858. Contributions to Helminthology. Proc. Acad. Nat. Sci. Phila., 10:110-112.

1888. Entozoa of the Terrapin. Proc. Acad. Nat. Sci. Phila., 40:128.

LINTON, E.

1905. Parasites of Fishes of Beaufort, North Carolina. Bull. Bur. Fish., 24:321-428, 34 pl.

LOOSS, A.

1885. Beiträge zur Kenntnis der Trematoden. Zeit. f. wiss. Zool., 41:390-446, 1 pl.

1892. Ueber *Amphistomum subclavatum* Rud. und seine Entwicklung. Festschr. Leuckart, p. 147-168, pl. 19-20.

1893. Ist der Laurer's Canal der Trematoden eine Vagina? Centr. f. Bakt. u. Par., 13:808-819.

1896. Recherches sur la Faune parasitaire de l'Égypt. Première partie, Mém. de l'Inst. égypt, 3:1-252, 16 pl.

1899. Weitere Beiträge zur Kenntnis der Trematoden-Fauna Aegyptens. Zool. Jahrb., Syst., 12:521-784.

1902. Ueber neue und bekannte Trematoden aus Seeschildkröten. Zool. Jahrb., Syst., 16:411-894, pl. 21-32.

1912. Ueber den Bau einiger auscheinend seltener Trematoden-Arten. Zool. Jahrb., Suppl., 15:323-366, 3 pl.

LÜHE, M.

1909. Parasitische Plattwürmer. 1, Trematodes. Die Süsswasserfauna Deutschlands, 17:1-217, 188 figs.

MACCALLUM, G. A.

1913. Fertilization and Egg-Laying in *Microcotyle stenotomi*. Science, n. s., 37:340-341.

MACCALLUM, G. A., and MACCALLUM, W. G.

1913. On *Aspidogaster ringens* and *A. kemostoma* n. sp. Zool. Jahrb., Syst., 34:245-256, 4 figs.

MACCALLUM, W. G.

1905. On Two New Amphistome Parasites of Sumatran Fishes. Zool. Jahrb., Syst., 22:667-678, 2 figs.

MACÉ, E.

1880. Des Trématodes parasites des Grenouilles. Bull. Soc. d'étud. scien. Finistère, Morlaix, 31 pp., 4 pl. (Cited after Braun, 1879-1893.)

MONTICELLI. F. S.

1892. *Cotylogaster michaelis* n.g., n. sp., e revisione degli Aspidobothridae. Festschr. Leuckart, p. 166-214, 2 pl.

1903. Per una nouva classificatione degli "Heterocotylea". Monit. zool. Ital., 14:334-337.

NICKERSON, W. S.

1895. On *Stichocotyle nephropis* Cunningham, a Parasite of the American Lobster. Zool. Jahrb., Anat., 8:447-480, 3 pl.

1902. *Cotologoster occidentalis* n. sp. and a Revision of the Family Aspidobothridae. Zool. Johrb., Syst., 15:597-624, 2 pl.

ODHNER, T.

1898. Über die geschlechtsreife Form von *Stichocotyle nephropis* Cunningham. Zool. Anz., 21:509-513.

1911. Zum natürlichen System der digenen Trematoden, I. Zool. Anz., 37: 181-191.

1911a. Zum natürlichen System der digenen Trematoden, IV. Zool. Anz., 38:513-531.

1912. Die Homologien der weiblichen Genitalwege bei den Trematoden und Cestoden. Nebst Bemerkungen zum natürlichen System der monogenen Trematoden. Zool. Anz., 39:337-351.

1913. Noch einmal die Homologien der weiblichen Genitalwege der monogenen Trematoden. Zool. Anz., 41:558-559.

OSBORN, H. L.

1898. Observations on the Anatomy of a Species of Platyaspis Found Parasitic on the Unionidae of Lake Chautauqua. Zool. Bull., 2:55-67, 6 figs.

1904. On the Habits and Structure of *Cotylaspis insignis* Leidy, from Lake Chautauqua, N. Y. Zool. Jahrb., Anat., 21:201-243, 3 pl.

OTTO, H. R.

1896. Beiträge zur Anatomie und Histologie der Amphistomiden. Dtsch. Zeit. Thiermed., 22:85-141, 30 figs.

POCHE, F.

1907. Einige Bemerkungen zur Nomenclature der Trematoden. Zool. Anz., 31:124-126.

POIRIER, J.

1886. Trématodes nouveaux ou peu connus. Bull. Soc. Philom. Paris, 7 sér., 10:20-40, 4 pl.

PRATT, H. S.

1900. Synopses of North American Invertebrates, XII. The Trematodes. Part 1. The Heterocotylea or Monogenetic Forms. Amer. Nat., 34:645-662, 50 figs.

1908. Parallel Development in Trematodes. Science, n. s., 27:489.

RUDOLPHI, C. A.

1801. Bebachtungen über die Eingeweidewürmer. Arch. f. Zool. u. Zootom., 2:1-65.

1809. Entozoorum sive vermium intestinalium historia naturalis. Amstelaedami, 1809.

1819. Entozoorum synopsis. Berolini, 1819.

ST. REMY, G.

1891. Synopsis des Trémotodes monogénèses Rev. Biol. Nord. France, 4:1-92, 2 pl.

1898. Complément du synopsis des Trématodes monogénèses. Arch. d. Paras., 1:521-571, 6 figs.

STAFFORD, J.

1896. Anatomical structure of *Aspidogaster conchicola.* Zool. Jahrb., Anat., 9:477-542, 4 pl.

1900. Some Undescribed Trematodes. Zool. Jahrb., Syst., 13:399-414, 1 pl.

1905. Trematodes from Canadian Vertebrates. Zool. Anz., 28:681-694.

STEWART, F. H.

1914. The Anatomy of *Polystomum kachugae* n. sp. with Notes on the Genus Polystomum. Rec. Ind. Mus., 10:195-205, 4 pl.

STIEDA, L.

1870. Ueber den Bau des *Polystomum integerrimum*. Arch. f. Anat. Phys. u. Med., 5:660-678, 1 pl.

STILES, CH. W., and GOLDBERGER, J.

1910. A Study of the Anatomy of *Walsonius watsoni* of Man and of Nineteen Allied Trematode Worms of the Superfamily Paramphistomoidea. Bull. Hyg. Lab., No. 60:1-264, 205 figs.

STILES, CH. W., and HASSALL, A.

1902-1912. Index-Catalogue of Medical and Veterinary Zoology. Bull. Bur. Animal Ind., No. 39.

1908. Index-Catalogue of Medical and Veterinary Zoology. Bull. Hyg. Lab., No. 37:89.

STUNKARD, H. W.

1916. On the Anatomy and Relationships of Some North American Trematodes. Jour. Par., 3:21-27.

TASCHENBERG, O. E.

1879. Zur Systematik der Monogenetischen Tematoden. Zeit. gesammt. Naturwissensch., 52:232-265.

TREUTLER, F. A.

1793. Observationes pathologico-anatomicae, auctariam ad helminthologiam humani corporis continentes. Diss. in praes. Ch. F. Ludwig. Lips. (Cited after Braun, 1879-1893.)

VOELTZKOW, A.

1888. *Aspidogaster conchicola*. Arb. zool.-zootom. Inst. Würzb., 8:249-292, 5 pl.

WALTER, E.

1893. Untersuchungen über den Bau der Trematoden. Zeit. f. wiss. Zool., 56:189-243, 3 pl.

WILLEMOES-SUHM, R. VON

1872. Zur Naturgeschichte des *Polystomum integerrimum* and *Polystomum ocellatum*. Zeit. f. wiss. Zool., 22:29-39, 1 pl.

WRIGHT, R. R.

1879. Contributions to American Helminthology. Jour. Proc. Canad. Inst., N. S., 1:1-23, 2 pl.

WRIGHT, R. R., and MACALLUM, A. B.

1887. *Sphyranura osleri*. Jour. Morph., 1:1-48, 1 pl.

ZEDER, J. G. H.

1800. Erster Nachtrag zur Naturgeschichte der Eingeweidewürmer von J. A. G. Goeze. Leipzig, 1800.

ZELLER, E.

1872. Untersuchungen über die Entwicklung und Bau des *Polystomum integerrimum* Rud. Zeit. f. wiss. Zool., 22:1-28, 2 pl.

1876. Weiterer Beitrag zur Kenntniss der Polystomen. Zeit. f. wiss. Zool., 27:238-275, 2 pl.

EXPLANATION OF PLATES

All figures except those of reconstruction were drawn with the aid of a camera lucida and were made from permanent mounts.

Abbreviations used

a	acetabulum
b	esophageal bulb
cm	circular muscles
cs	cirrus sac
e	esophagus
ed	excretory duct
ep	excretory pore
gp	genital pore
gc	genito-intestinal canal
h	small hooklets
hd	hermaphroditic duct
i	intestine
l	Laurer's canal
lm	longitudinal muscles
ls	lymph sinus
lt	limiting membrane
m	mouth
md	median dorsal lymph canal
mg	Mehlis' gland
mo	marginal organ
mt	metraterm
mv	median ventral lymph canal
nc	nerve commissure
o	ovary
oc	eye spot
od	oviduct
om	oblique muscles
oo	ootype
op	oral evagination
os	oral sucker
ov	egg
p	postate gland
ph	pharynx
sp	septum
sv	seminal vesicle
t	testis
u	uterus
ud	uterine duct
v	vitellaria
vd	vas deferens
vg	vagina
vl	vitelline duct
vv	vitello-vaginal canal

PLATE I

EXPLANATION OF PLATE

Polystoma orbiculare

Fig. 1. Entire specimen, extended, ventral view. × 35.
Fig. 2. Hook from genital coronet. × 225.
Fig. 3. Reconstruction of genital apparatus from frontal sections. × 135.
Fig. 4. Sagittal section thru caudal disc. × 87.
Fig. 5. Frontal section thru caudal disc. × 73.
Fig. 6. Sagittal section thru oral sucker and pharynx. × 140.

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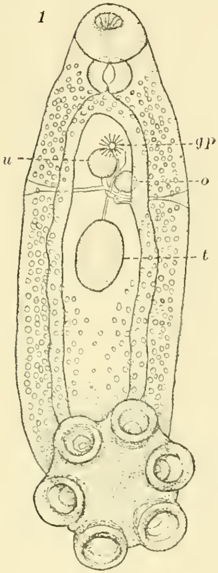

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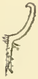

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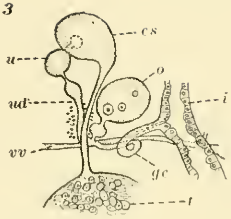
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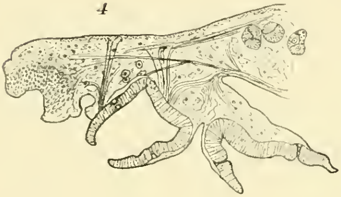

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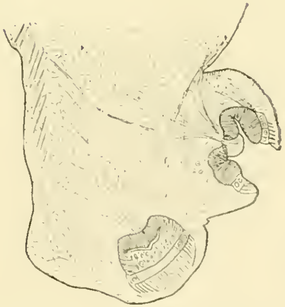

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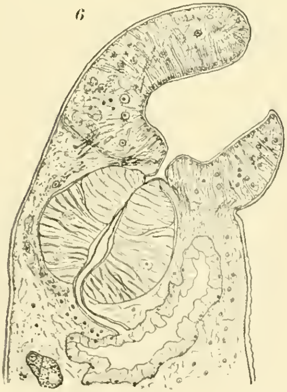

STUNKARD NORTH AMERICAN POLYSTOMIDAE PLATE I

PLATE II

EXPLANATION OF PLATE

Polystoma orbiculare

Fig. 7. Frontal section. × 35.

Fig. 8. Frontal section of ootype and beginning of uterine duct. × 185.

Fig. 9. Frontal section of ootype and end of right vitello-vaginal canal, five sections ventral to Figure 8. × 185.

Fig. 10. Frontal section, oötype region of same specimen as Figures 8 and 9, showing ovary, uterus, oviduct, uterine duct, genito-intestinal canal and vas deferens. × 140.

Fig. 11. Frontal section showing vitellaria and origin of vitelline ducts with granular secretion in the cells and duct. × 87.

Fig. 12. Frontal section thru cirrus sac at the juncture of the shanks and roots of the genital hooks, showing the genital papillae cut across, and a section of the duct from the uterus at the bottom of the figure. × 250.

Fig. 13. Reconstruction of male genital apparatus from sagittal sections. × 140.

Fig. 14. Frontal section thru uterus showing embryo in stage of a morula-like mass of cells. × 700.

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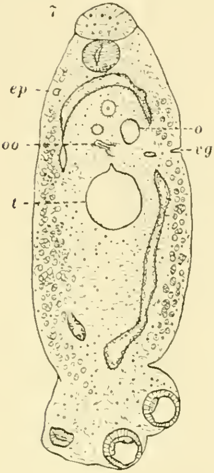

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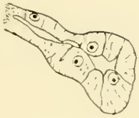

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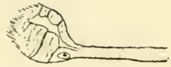

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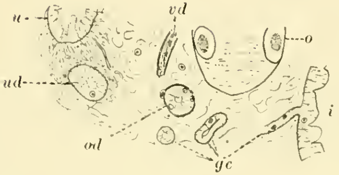
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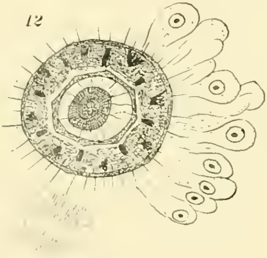

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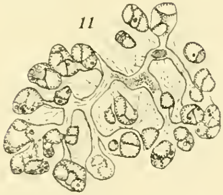

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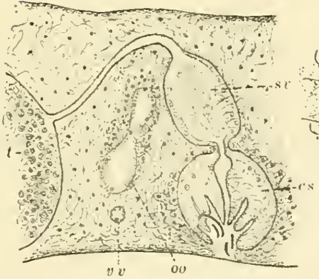

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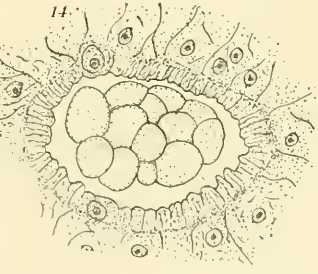

PLATE III

EXPLANATION OF PLATE

Polystoma opacum

Fig. 15. Entire specimen, extended, ventral view. × 20.
Fig. 16. Reconstruction of genital apparatus from toto preparation and cross sections. × 50.
Fig. 17. Hook from genital coronet. × 550.
Fig. 18. Frontal section thru the anterior sucker and pharynx, showing in section nerve commissures and vitellaria. × 60.
Fig. 19. Cross section of body thru uterus and cirrus sac. × 60.
Fig. 20. Cross section of body thru the testis. × 60.
Fig. 21. Cross section thru the anterior pair of bothria. × 60.

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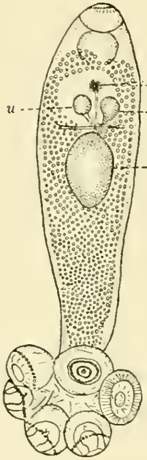

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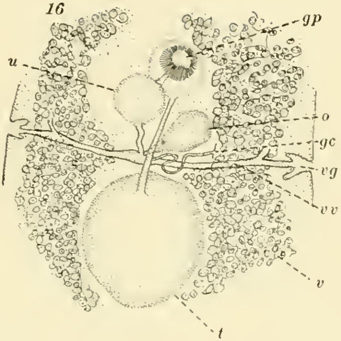
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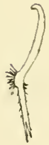

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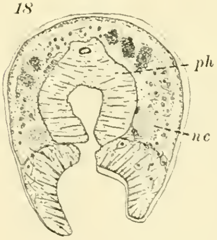

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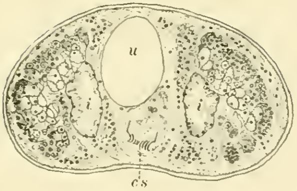

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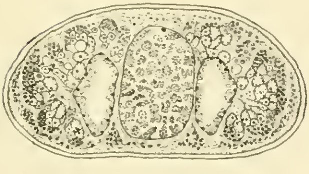

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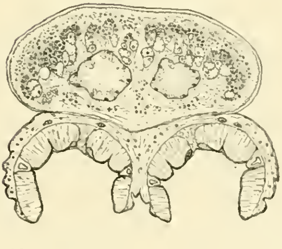

PLATE IV

EXPLANATION OF PLATE

Polystoma megacotyle

Fig. 22. Entire specimen, ventral view. × 27.
Fig. 23. Cross section of body thru ovary and uterus. × 60.
Fig. 24. Cross section of body thru vaginae and anterior part of the testis. × 60.
Fig. 25. Cross section thru the pharynx near the posterior end. × 85.
Fig. 26. Cross section of seminal vesicle and cirrus sac. × 140.

Polystoma coronatum

Fig. 27. Entire specimen, ventral view. × 27.

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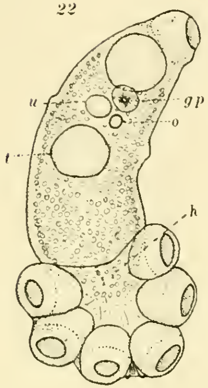

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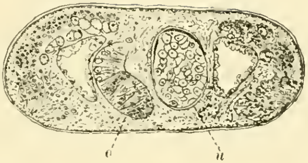

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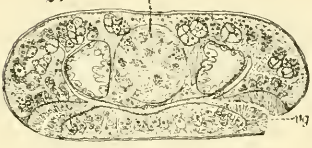

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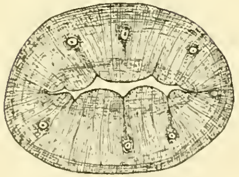

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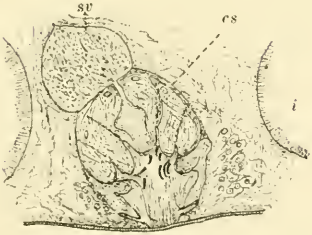

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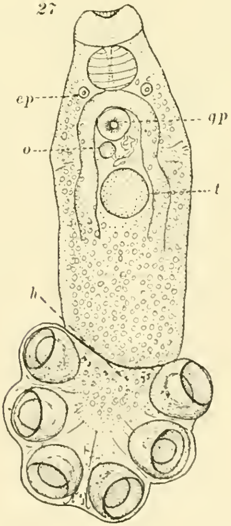

STUNKARD NORTH AMERICAN POLYSTOMIDAE PLATE IV

PLATE V

EXPLANATION OF PLATE

Polystoma microcotyle

Fig. 28. Entire specimen, ventral view. × 27.

Fig. 29. Ventral view of caudal disc, showing arrangement of musculature and hooks. × 43.

Polystoma hassalli

Fig. 30. Entire specimen, ventral view, ceca connected posteriorly. × 45.

Fig. 31. Entire specimen, ventral view, in which there is no posterior connexion between the ceca. × 40.

Fig. 32. Reconstruction of genital apparatus from frontal sections. × 135.

Fig. 33. Frontal section thru the dorsal part of the uterus, showing oral sucker, pharynx, nerve commissures, intestine, excretory vesicles and ducts, vitellaria and smaller tubes of the ootype region. × 60.

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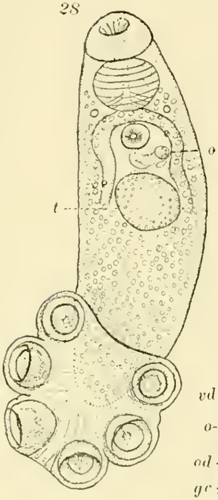

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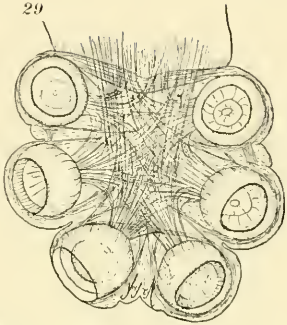

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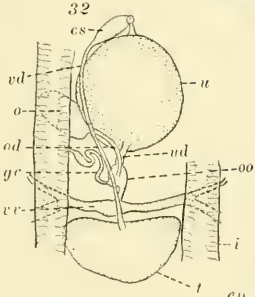
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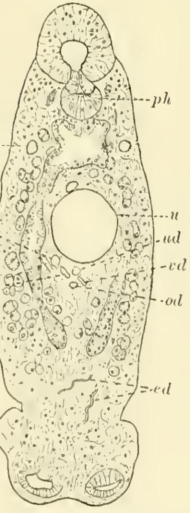
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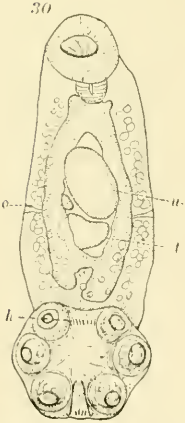

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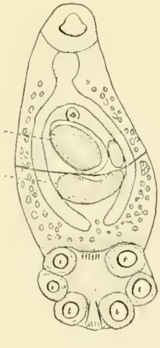

PLATE VI

EXPLANATION OF PLATE

SUCKERS AND HOOKS OF VARIOUS SPECIES OF POLYSTOMES

Fig. 34. *Polystoma orbiculare*, bothrium from caudal disc. × 140.

Fig. 35. *Polystoma orbiculare*, frontal section thru bothrium. × 140.

Fig. 36. *Polystoma obiculare*, optical section of bothrium showing cuticular framework. × 140.

Fig. 37. *Polystoma opacum*, hook from base of sucker. × 165.

Fig. 38. *Polystoma opacum*, hook from anterior margin of caudal disc. × 165.

Fig. 39. *Polystoma microcotyle*, hooks of posterior margin of disc. × 165.

Fig. 40. *Polystoma opacum*, hooks of posterior margin of disc. × 165.

Fig. 41. *Polystoma megacotyle*, hooks of posterior margin of disc. × 165.

Fig. 42. *Polystoma coronatum*, hooks of posterior margin of disc. × 165.

Fig. 43. *Polystoma orbiculare*, hook from base of sucker. × 165.

Fig. 44. *Polystoma orbiculare*, frontal section thru a sucker illustrating the method of operation; the external zones are retracted with the resulting protrusion of the basal part. × 140.

Fig. 45. *Polystoma integerrimum*, frontal section thru a sucker showing type of cuticular framework. Compare with text and types illustrated in other figures. × 100.

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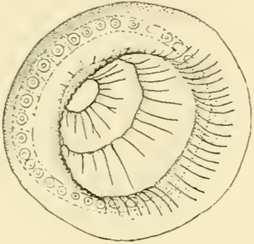

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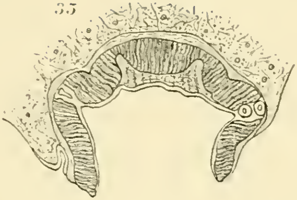

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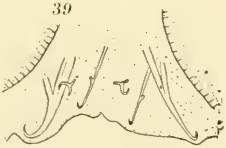

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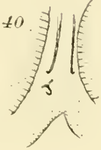

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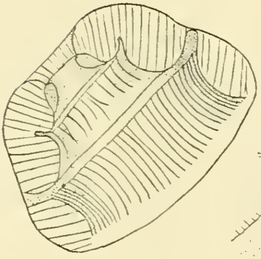

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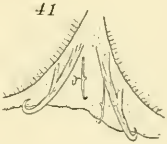

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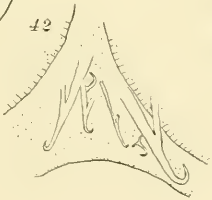

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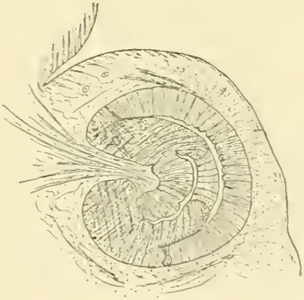

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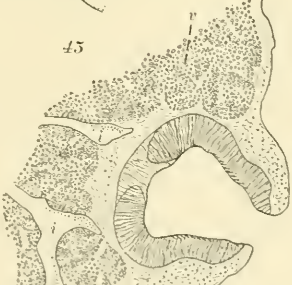

PLATE VII

EXPLANATION OF PLATE

Cotylaspis cokeri

Fig. 46. Entire specimen, extended, dorsal view. × 40.

Fig. 47. Ventral view of entire specimen showing position of marginal organs and divisions of the adhesive disc. × 40.

Fig. 48. Reconstruction of reproductive organs from frontal sections. × 80.

Fig. 49. Cross section of body at the level of the ovary showing the ovary, uterus, seminal vesicle, intestine, excretory ducts, and a follicle of the vitellaria. × 87.

Fig. 50. Diagrammatic representation of the excretory system from a living specimen, dorsal view. × 40.

Fig. 51. Oblique section of body just posterior to the genital pores, showing in section the mouth funnel, pharynx, cirrus sac, uterus, septum and adhesive disc. × 87.

Fig. 52. Entire specimen, contracted, dorsal view. × 40.

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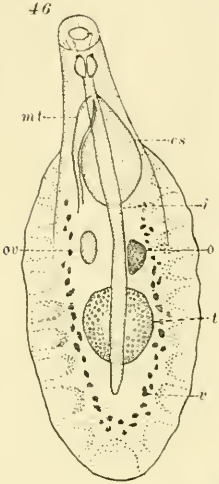
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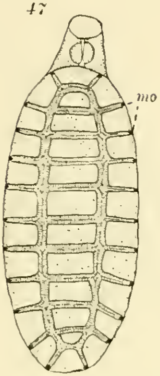

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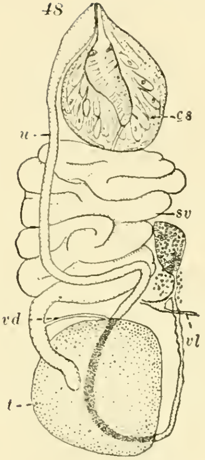
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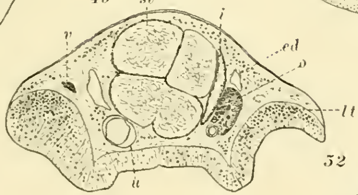
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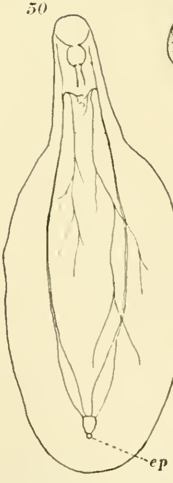

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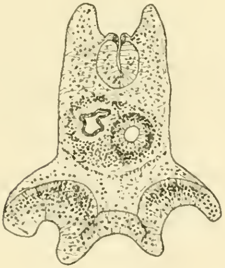

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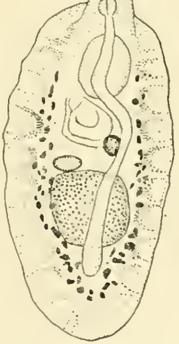

PLATE VIII

EXPLANATION OF PLATE

Cotylaspis cokeri (except Figure 56)

Fig. 53. Sagittal section thru the anterior end of body showing musculature, digestive and reproductive organs. × 200.

Fig. 54. Frontal section thru the openings of the genital pores. × 85.

Fig. 55. Section thru a marginal organ; a muscle fiber is seen at the left of the figure and on the other side a nerve fibril passes to the inner end of the thick walled part of the canal. In this section the canal is cut across and can not be traced from the bulb to the exterior. × 580.

Fig. 56. Section thru a marginal organ in *Cotylaspis insignis.* × 580.

Fig. 57. Frontal section thru the adhesive disc showing arrangement of musculature. × 95.

Fig. 58. Section thru the anterior part of the forebody showing the base of the mouth funnel, anterior part of the pharynx, nerve commissure and eye spots. × 800.

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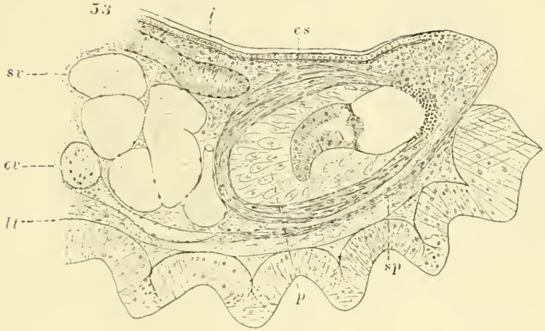
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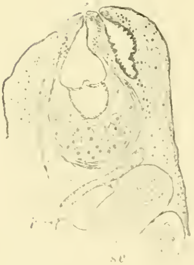

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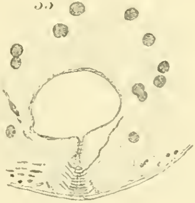

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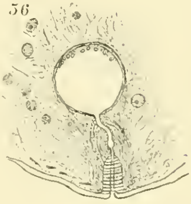

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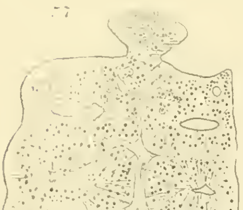

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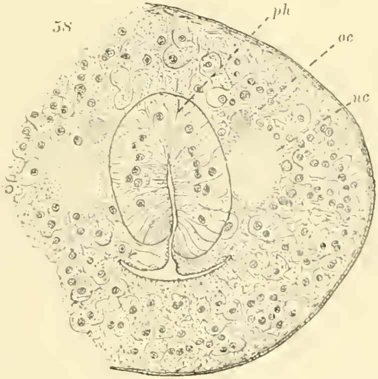

PLATE IX

EXPLANATION OF PLATE

Alassostoma magnum

Fig. 59. Entire specimen, ventral view. × 9.

Fig. 60. Cross section thru the genital pore showing the terminal parts of the cirrus sac and uterus, the hemaphroditic duct, genital sinus, four layers of muscles in the body wall and the muscle lamellae of the esophageal bulb. ×27.

Fig. 61. Diagrammatic representation of female genital apparatus reconstructed from cross sections. ×40.

Fig. 62. Section of the wall of the intestine. ×360.

Fig. 63. Cross section thru the oral sucker and the oral evaginations. × 40.

Fig. 64. Cross section of body at the level of the ovary showing in section the ovary, uterus, Laurer's canal, the ceca, vitellaria, lymph spaces and excretory ducts. × 16.

Fig. 65. Cross section thru the oral sucker showing arrangement of muscle fibers and position of the nuclear zone. × 35.

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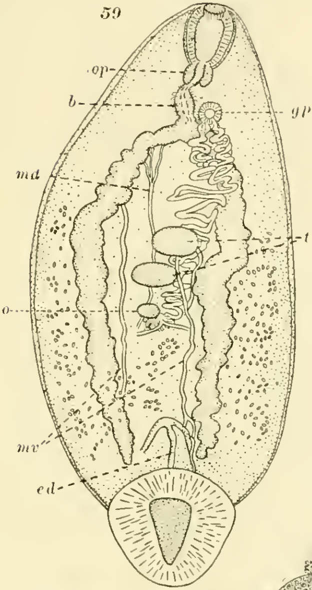
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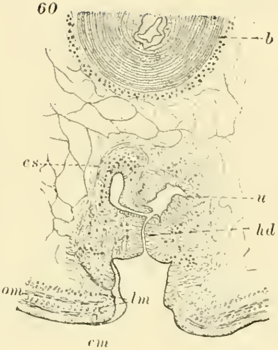
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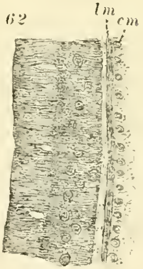

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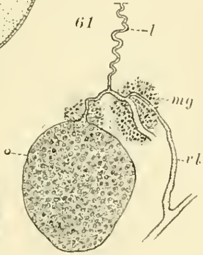

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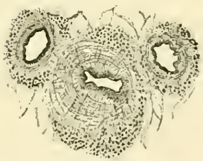

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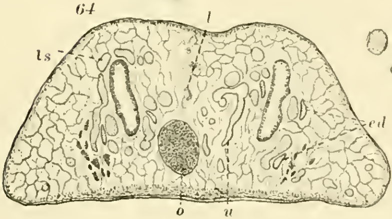

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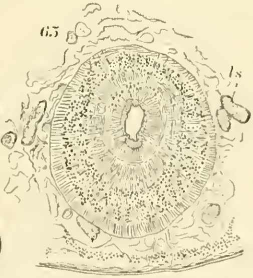


STUNKARD NORTH AMERICAN PARAMPHISTOMIDAE PLATE IX

PLATE X

EXPLANATION OF PLATE

ALASSOSTOMA PARVUM

Fig. 66. Entire specimen, ventral view. × 27.

Fig. 67. Cross section of body posterior to the ovary showing coils of the excretory ducts. × 70.

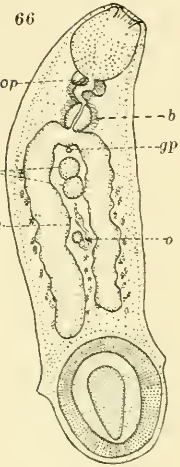
Fig. 68. Cross section thru the posterior part of the acetabulum showing lymph spaces around the sucker. × 70.

Fig. 69. Cross section a short distance posterior to the genital pore showing in section, the uterus, the cirrus sac, and above the latter organ three loops of the seminal vesicle. × 70.

Fig. 70. Cross section of esophageal bulb with clusters of surrounding cells. × 70.

Fig. 71. Cross section of body thru the genital pore showing hermaphroditic duct, cirrus sac, lymph spaces and the character of the parenchyma. × 90.

66



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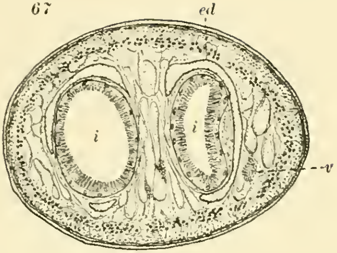

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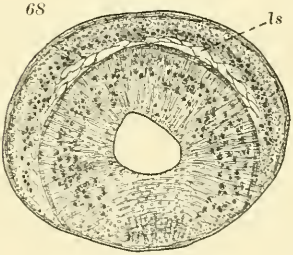

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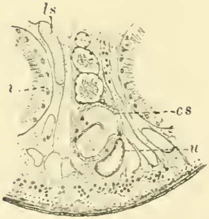

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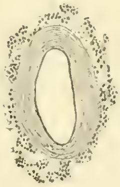

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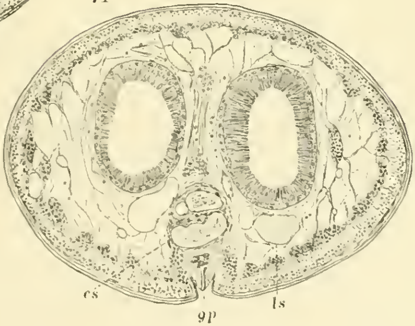


PLATE XI

EXPLANATION OF PLATE

Zygocotyle ceratosa

Fig. 72. Entire specimen, ventral view. × 11.

Fig. 73. Cross section of esophageal bulb, showing the arrangement of the muscle fibers. × 45. Compare with Figures 60 and 70.

Fig. 74. Cross section of body thru the origin of the oral evaginations. × 45.

Fig. 75. Sagittal section thru the anterior part of the body showing oral sucker, an oral evagination and the anterior part of the esophagus. × 45.

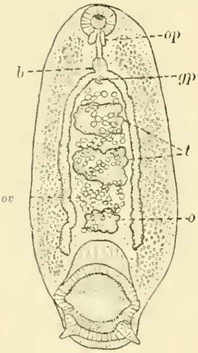
Fig. 76. Sagittal section of posterior part of body thru one side of the acetabulum. × 27.

Fig. 77. Sagittal section of the posterior part of the body near the median line, showing the ovary, eggs in the uterus, Laurer's canal, and the shape of the acetabulum. × 27.

Fig. 78. Sagittal section thru the body one section at the side of the genital pores showing the folded wall of the uterus and the ejaculatory duct which in this species is without a cirrus sac. × 136.

Fig. 79. Representation of the sagittal section thru the openings of Laurer's canal and the excretory vesicle. × 90.

72



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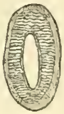

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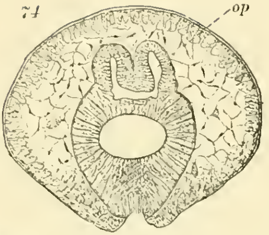

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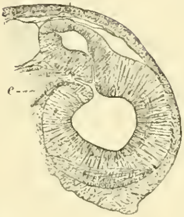

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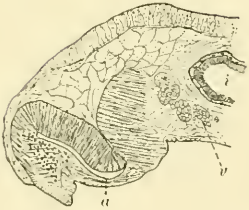

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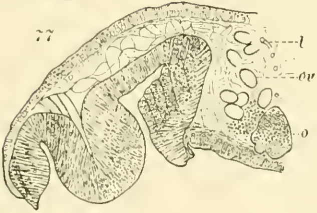

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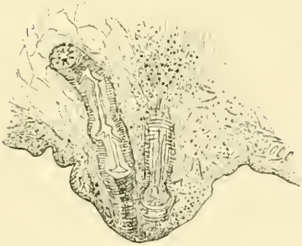

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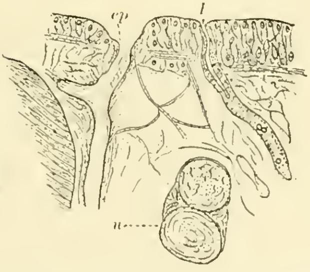

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COLOR AND
COLOR-PATTERN MECHANISM
OF TIGER BEETLES

WITH TWENTY-NINE BLACK AND
THREE COLORED PLATES

BY

VICTOR E. SHELFORD

Contributions from the
Zoological Laboratory of the University of Illinois, No. 93

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INTRODUCTION

In the analysis of characters made the basis of studies of variation, orthogenetic trends, experimental modification and heredity, noteworthy advantages are associated with the study of large groups of species in which divergence and modification have proceeded in various directions. The material should be plastic so that the laws governing response in characters can be determined. The ontogeny of the characters should be of such a character as to show the general ground plan of the system and its relation to the existing adult characters and their variations. It is further desirable to be able to breed the organism, segregate pure lines, and cross various species. There is a strong tendency of late years to regard the breeding and the breeding results as superior to the other attempts at character analysis. This has proceeded to such an extent without adequate physiological analysis that one writer (Riddle, 1909) designated the method of cross breeding "the mixing of unknowns". The primary object of this paper is to show the nature of the color and color-pattern mechanism of the elytron.

In the matter of qualifications of material the tiger beetles are admirably adapted to all the needs enumerated above, but since one year at least and normally two are necessary for a generation, only a few single generations have been bred. For this reason the idea of breeding them was abandoned. It is also a purpose of this paper to show that breeding is not the only method by which adequate analysis can be reached, i.e., unless the laws governing heredity are a system entirely a part from those governing the modification of parts during ontogeny and the normal course of variation, which seems to be the tacit assumption of various students of heredity in the not too distant past.

I shall indicate further that orthogenetic tendencies, if directive tendencies are to be so named, are numerous and in a large series of species present a confusing set of groups which are excessively complicated and reduced to any simple system, as claimed by Eimer and von Linden for Lepidoptera or for a limited number of species by Whitman, with difficulty. Still, large tendencies with numerous minor ones within them may be detected. It will be shown that the laws governing the modification of patterns apply alike to general, probably hereditary tendencies and detailed responses under experimental conditions. It will be shown that biogenetic law must be applied with caution and is not of such broad application as is held in some quarters, being inapplicable to various characters altogether.

The brilliant colors of the group are due to physical phenomena determined by Professor Michelson, and leave no place for the biogenetic law in connection with the development of color during ontogeny. It will be shown further that color is closely correlated with general physiological condition and is modifiable by conditions which affect general metabolism. The results here presented are based on several years of observation.

In 1903 the writer undertook a study of variation of the tiger beetles. The work here presented is the outgrowth of this beginning, and indeed includes some small portions regarding color patterns that were written in that year. The work has been prolonged for many reasons, but chief of these was the very large number of species in the group and the fact that an adequate understanding of the material could not be attained without consulting many large collections. Further, the experimental results obtained in 1906 demanded a first-hand study of the variations of the species concerned and their natural habitats. The accumulation of material and data was not completed until 1911. Some of this had to be studied, drawings made, etc., which with numerous other duties and enterprises under way made necessary much time to put it into the present form.

A family with upwards of 1300 species of which more than 600 are in one genus and with characters which can be studied and analyzed, appeared to afford material which was sufficiently promising to justify delay. In the fourteen years that have elapsed since the problem was first undertaken at the suggestion of Dr. C. B. Davenport, the attention of biologists has shifted from variation, which was then the chief topic of interest, to experimental modification of characters, and finally to the methods of modern genetics. Various men have made numerous suggestions regarding the work, but in its final preparation the writer has been able to use only a few of them in a general way, and an attempt is made to present the facts and conclusions growing out of the material as simply as possible.

MATERIALS AND METHODS

The material which has been used as the basis of this work has consisted of collections in the family Cicindelidae of the world, extensive collections of several North American species, repeated year-to-year collections of a few species in Illinois and Indiana, series of observations on the ontogeny of color in a small number of North American species, and experimental modification of a number of species which has assisted in the analysis of the color patterns.

The collections studied have covered most of the species of the family, which is divided into several tribes by W. Horn in the Genera Insectorum (1915). The subfamilies herein named were in part given as families in the Systematischer Index of the same author (1906), in which he presented a preliminary list of the species which he later published in the Genera Insectorum. Accordingly, in my previous papers on the subject (1906, 1908, 1912, 1914, 1915) the "Index" was followed almost entirely in the matter of nomenclature and order of arrangement.

The groups represented in the family as outlined in Genera Insectorum are as follows:

Subfamily Ctenostomini (tree dwellers)	Number of species
Pogonostoma; Madagascar	32
Ctenostoma; tropical America	45
Subfamily Collyrini (nearly all tree dwellers)	
Tricondyla; India	27
Collyris; Oriental region	104
Subfamily Manticharini (ground dwellers)	
Mantica; Africa	1
Manticora; Africa	5
Subfamily Megacephalini (ground dwellers)	
Platychila; South Africa	1
Pycnochila; South America	1
Amblychila; Western U. S. A.	2
Omus; Western U. S. A.	4
Aniaria; Northeastern South America	1
Megacephala; southern U. S. to Argentine, Africa, Arabia, Persia, Australia	68
Oxychila; middle America	25
Pseudoxychila; Andes, Costa Rica to Bolivia	1
Chiloxia; Andes of Ecuador to Bolivia	1
Eucallia; Andes of Ecuador and Columbia	1
Subfamily Cicindelini; ground dwellers	
Dromica; southern half of Africa	82
Prothyma; Africa, Madagascar, Asia, and the Malay Archipelago	50
Dilatotarsa; Malay Archipeligo	1
Caledonomorpha; New Guinea	1
Distipsidera; Australia and New Guinea	8
Caledonica; New Guinea	9

Nickerlea; Australia	2
Rhysopleura; Australia	1
Euprosopus; Brazil	2
Langea; Peru	1
Iresia; continental tropical America	8
Therates; Malay Archipelago	33
Odontochila; South America, Malay Pen. and Islands	75
Prepusa; South America)	3
Oxygonia; South America	15
Opisthencentrus; Brazil	1
Cicindela; world-wide distribution	686
Eurymorpha; Africa	1
Apteroessa; India	1
	1299

The group contains some 35 genera and upwards of 1300 species and subspecies. In the figures above the subspecies of Cicindela numbered in Roman in Horn's Genera Insectorum list, which number 55, are included, but subspecies numbering more than 8 in Megacephala alone, and several in other genera, are not included.

There are very few of these 1300 races which the writer has not seen in some one of the particularly numerous and complete collections studied. Those studied quite completely are: British Museum of Natural History; Hope Collection, Oxford University; Cambridge University; Private Collection of Mr. Basil G. Nevinson, London; Private Collection of Dr. Walther Horn, Berlin; Zoologisches Museum, Berlin; Private Collection of Doctor Gestro, Genoa; Jardin des Plantes, Paris; Museum of Comparative Zoology, Cambridge, Massachusetts; United States National Museum; Philadelphia Academy of Science: American Museum of Natural History, New York; and the University of Chicago collection including an old collection once the property of John Akhurst, Brooklyn, several purchases from Hermann Rolle of Berlin, and the material secured by exchange for other species in the Akhurst collection, and material purchased and collected for the writer by the University, and specimens collected on the excursions supported by the University. In addition to this the writer secured a collection of exotic material from Mr. John D. Sherman in exchange for Dytiscidae and numerous specimens by exchange and gift from numerous American and foreign collectors. Of the few species not seen several are represented in figures which show the color patterns.

Many of the drawings presented are from the collections in question and are appropriately designated in the groups of figures in the succeeding pages. The meaning of the designations is as follows: B, British Museum; C, Cambridge University; D, Berlin; G, Gestro; H, W. Horn, Berlin; M, U. S. National Museum; N, Nevinson; O, Oxford University; P, Paris; S, Shelford; U, University of Chicago.

While none of the patterns of the genera other than Cicindela are of a type differing from the general plan of the Cicindela, patterns are very often wanting or very simple, such as the simple cross bands in Collyris. In course of the examination of the several collections named, a great abundance of variation has been noted in some of the commoner representatives of the groups, not only of Cicindela but others also.

The taxonomic arrangement of Cicindela by Doctor Horn in the Genera Insectorum is especially fortunate. He has arranged the species into a number of groups on the basis of the distribution of hairs on the head, thorax, abdomen, tarsi, labrum, and of other structural characters, but without reference to color patterns. He gives 174 groups apparently not duplicated in the different regions and 16 represented in more than one zoogeographic region by the same or closely related species. These 174 groups are distributed as follows: Ethiopian region, 34; Oriental region, 48; Australian region, 22; Palearctic region which he extends to include China, 20; Nearctic region, 24; Neotropical region, 26. The groups found in more than one region and which are counted in the one with most species, are as follows:

TABLE I

Showing the Number of Species in Regions by Groups as Designated by a Common Species

	Ethiopian	Oriental	Australian	Pale-arctic	Nearctic	Neo-tropical
singularis Chd.	1	2		5		
melancholica Fab.	21	7		5		
donegalensis Chd.	4	2		6		
nilotica Dj.	1	1				
germanica L.	70			4		
foveolata Schm.		1	1			
laetescripta Mtsch.		1		1		
10 guttata Fab.		3	1			
striolata Illig.		2	1			
discreta Schm.		2	1			
semicincta Br.		1	3			
brevisponosus W. Horn		3		1		
carthagena Dej.					16	6
argentata Fabr.					6	8
trifasciata Fabr					1	3
macrocnema Chd.					3	2

In the above list species occurring in two are counted in both. So far as practicable these pilosity groups have been considered in working up, arranging, and discussing the patterns.

Considerable change has been made in the nomenclature and arrangement of species in the Genera Insectorum as compared with Doctor Horn's Index. The paper had progressed so far with the Index as a basis that it was thought not to be practicable to change it to agree with the newer work.

The extensive collection of North American species belong to the first group in Horn's series for the Nearctic region. This group includes *tranquebarica* and will be referred to as the *Tranquebarica* Group. These are characterized as follows: The four anterior trochanters have fixed hairs, cheeks naked, or with isolated hairs, clipeus often hairy. Frons with discoidal or supraorbital hairs; median portion of the frons never proportionately supplied with more or less short, close lying, downward directed hairs; frons never hairy above the antennal insertion. The disc of the middle frons is often hollowed out or sharply separated from the fore frons by its steepness. The first antennal segment is often thickly covered with outstanding hairs. The pronotum has at least rudimentary hairs, often circumdiscally and discally hairy; hairs often long and fine and never decumbent except when very numerous; free anterior and posterior border of the pronotum not hairy. The prosternum is always naked. The lateral portion of the breast is always thickly covered with hairs. The hind border of the femur and sometimes the foreborder also covered with fine short decumbent hairs; hook-formed hairs never present; hairs on the hip and superorbital border most numerous. This group stands in close relation to the European group to which *campestris* belongs. The main group includes *formosa*,* *venusta*, *limbata*, *purpurea*,* *ancosisconensis*, *duodecemguttata*,* *hirticollis*,* *latesignata*, *tranquebarica*,* *tenuicincta*, *bellissima*, *longilabris*, *eureka*, *oregona*, *senilis*, *willistoni*, *fulgida*, *pulchra*, *pimeriana*, *scutellaris*.* In addition to this, collections were made of C. *sexguttata* which stands in a group by itself. Those starred were studied especially. Collections of these species representing complete catches were supplied by C. S. Brimley, E. G. Smyth, C. A. Frost, L. H. Joutel, Rev. J. C. Warren, and Dr. C. F. Adams. Collections were made by the writer in various parts of the United States.

The species about Chicago, especially *scutellaris*, were collected through the year from the same locality with a view to getting the seasonal variation of the species and any variation from generation to generation.

The color ontogeny work was done on material dug in the larval stage at Glencoe, Illinois (*C. limbalis*); at Gary, Indiana, (*C. tranquebarica*); at Miller, Indiana (*C. lecontei*): at Lyons, Illinois (*C. purpurea*); at East Chicago, Indiana (*C. repanda*); Chicago vacant lots (*C. punctulata*); and Suman, Indiana (*C. sexguttata*). These larvae were reared in a greenhouse in which the temperature was about 4 to 8 degrees C. higher than the out-door soil temperature. This accelerated the appearance only a little and did not show modification of color or pattern. The larvae were reared in sand, either in cylindrical lamp chimneys, setting in screen bottomed boxes or in screen bottomed boxes. When the majority of larvae and pupated all were removed to small square watch glasses, lined with filter paper and moistened with 2% H_2O_2. These were piled up so as to cover each other and kept in a cool room, and watched closely to secure as many as practicable at the time of emergence. The elytral material was nearly all killed in a picro-sulfuric acid killing fluid and cleared and mounted in balsam, but some was preserved in glycerine jelly direct with good results. They were preserved at different intervals after emergence.

The material for experiments was collected from the same places as that for ontogeny study and was subjected to high and low temperatures in an apparatus to be described later.

The writer is indebted to Dr. C. B. Davenport, the late Professor C. O. Whitman, Professor C. M. Child, and Professor W. L. Tower for suggestions during the first four years of the work (1903-1907). He is further indebted to the University of Chicago for funds amounting to $400 and to Professor and Mrs. F. R. Lillie for funds amounting to $200 to cover expenses connected with the study and collection of the group. The Graduate School and Department of Zoology of the Univesity of Illinois provided for later stages of the work.

Acknowledgments are due Miss Annette Covington for making the water color drawings of the ontogenetic stages and the other changes in color during the life history. Mr. K. Toda made the drawings of the geographic races shown in color and also the stippled drawings of ontogeny.

The writer is especially indebted to Professor A. A. Michelson of the University of Chicago for making physical determinations of the colors of Cicindela. The courtesies connected with the study of collections were numerous. The following were especially kind in facilitating the study of collections in their charge: Dr. Samuel Henshaw, Museum of Comparative Zoology; Dr. Schwarz, U. S. National Museum; Dr. Henry Skinner, Philadelphia Academy; Mr. William Beutenmuller, American Museum; Mr. Gilbert I. Arrow and Mr. C. J. Gahan, the British Museum; Professor Poulton and the late Mr.

R. Shelford, Hope Collections, Oxford; Professor David Sharpe, Cambridge; Professor Kolbe, Berlin; Mr. P. Lesne, Paris.

The following permitted me to study their private collections with a considerable loss of time and attention: Dr. Walther Horn, Berlin; Mr. Basil G. Nevinson, 3 Tedworth Square, London; Mr. Gestro, Genoa.

A considerable number of men whose names appear below gave me data on the distribution of the species in their collections, loaned or presented specimens, or did similar service through making extensive collections which were exchanged. For this I am debtor to Messrs. C. F. Adams, C. N. Ainslie, Geo. G. Ainslie, E. M. Anderson, A. W. Andrews, Germain Beaulieu, Biederman, Wm. Beutenmuller, Albert L. Barrows, C. S. Brimley, T. C. Brues, T. D. A. Cockerell, I. W. Cockle, Norman Criddle, F. F. Crevcoeur, C. C. Deam, G. M. Dodge, Edwin H. Edwards, J. D. Evans, S. A. Forbes, E. P. Felt, E. D. Harris, R. V. Harvey, G. W. Herrick, H. R. Hill, J. S. Hine, A. D. Hopkins, W. Horn, James Hunsen, S. A. Johnson, James Johnson, W. Knaus, Chas. W. Leng, H. P. Loding, D. E. Lantz, W. MacIntosh, G. P. Mackenzie, L. E. Marmont, A. L. Melander, F. W. Nunenmacher, W. E. Rumsey, L. E. Ricksecker, A. G. Ruthven, Franklin Sherman, H. F. Snow, E. G. Smyth, Tom Spalding, Chas. Stevenson, T. B. Symons, H. B. Walden, H. F. Wickham, T. N. Willing, R. S. Woglum, R. H. Wolcott, E. O. Wooton, E. C. VanDyke, E. P. Venables, S. S. Visher.

ANALYSIS OF COLOR PATTERNS

COLOR PATTERNS AND ELYTRAL STRUCTURES

In the Cicindelidae usually only the elytra have color patterns. These are merely sack like outgrowths supplied with nerves, trachea, and blood spaces. The cuticular covering is in two layers; the outer portion is a hard and relatively homogeneous layer known as the *primary cuticula* and on the upper side is usually characterized by the presence of saucer-shaped depressions, somewhat hexagonal in form, fitting together with common rims. These rims usually correspond to the positions of the points of contact of the hypodermal cells and accordingly each cup corresponds to a cell (Packard, 1900 text). Some forms in the family, e. g., the Tetrachas and the Amblychilas do not have these cups; the surface is smooth. In certain areas the primary cuticula is pigmented and in certain areas clear and transparent. This gives the color pattern. Some species are almost entirely pigmented; some entirely without pigment. Beneath the primary cuticle is the secondary cuticula which is laid down in successive layers during the life of the individual and in the forms like *Amblychila cylindriformis*, and *Phaeoxantha klugi* is essentially uniform in character. It contains some spaces, probably pore canals, which are empty of cell contents except for the layer in actual contact with the cells. A few of these pore canals can be detected in the secondary cuticula of *Tetracha carolina*. In Cicindela the secondary cuticula beneath the pigmented areas of the elytron is clear and transparent and entirely free from the "pore canals" and interlamellar spaces, while beneath the unpigmented areas it is full of the "pore canals" and large interlamellar spaces, and these having been left empty by the retreat of the cells from the successive layers; they give the effect of a white or straw color depending upon the color of the secondary cuticula itself. In these regions, beneath the unpigmented primary cuticula, it is about twice as thick as beneath the pigmented parts (Fig. 1, Pl. I). The color pattern may accordingly be described in terms of pigment and lack of pigment, the so-called markings being without pigment.

The two walls of the sac-like elytron are held together by chitinous pillars or columns which in the adult appear in cleared elytra. The different layers of cuticula show here as rings around the original central spindle (Shelford 1915:243, Fig. 1). In the Cicindelidae the chitinous columns are not arranged in any very definite manner but in some cases they retain their pigment within areas that are not otherwise pigmented.

Hairs which in a primitive insect usually cover the wing entirely are present in nearly all tiger beetle elytra. In the Mantichoras, observed representative of the Pogonostomidae, and one of the Megacephalidae, *Megacephala* (*Tetracha*) *aequinoctialis,* the elytra are more or less completely and uniformly covered with small hairs. Under the microscope the hairs may be located on the pigmented area of the elytra by the light area which is produced by the thin cuticula at the base of each hair. Hairs appear on the whole to be less common in the unpigmented areas and when present usually are surrounded by a narrow rim of pigmented cuticula. Hairs occur in practically all groups, though they have been lost from the majority except for a few at the base of the elytron and scattered along the tracheae (Shelford, 1915:243, Figs. 1 to 3). These are present in Cicindela and are shown by small circles in figures 2 to 29, plate I to III.

The elytra of many species are marked with pits. Close examination under the microscope with both transmitted and reflected light shows that, in the majority of cases, the pits are over the center of the chitinous columns and bear no relation to rudimentary hairs as Dr. W. Horn has suggested. I have seen no pits that would appear to represent rudimentary hairs though they may occur.

There are sometimes thickenings running lengthwise of the elytron as in Domica (Shelford, 1915: Figs. 35 and 36). While these thickenings run parallel with the trachea, they are usually between rather than coincident with them, except in Caledonica (Fig. 25). There are, however, some thickenings on the under side of the elytra of most species which correspond in a general way to veins (particularly in Mantichora). The outer and inner margins of the elytra are always thickened and resemble veins, almost invariably containing tracheae. The subcosta usually follows the costa very closely at the base of the elytron but just behind the middle it turns inward away from the margin in a vein like thickening. The radius is in a distinct thickening of the elytron which proceeds from the base for a short distance. This is very constantly present. Aside from this nothing comparable to veins is present but the rows of chitinous columns are often so arranged so as to give distinct and direct spaces running the length of wing. These are occupied by the principal tracheae. In some cases the spaces appear very clearly on the under side of the elytron and in Mantichora there are distinct ridges over them which have every appearance of veins.

The elytral tracheation of the Cicindela has been observed by the writer in about one hundred species. The elytra of the newly emerged imagoes of ten North American species have been studied in some detail. Nearly all the common North American species and about fifty exotic species have been studied in less detail by mounting dried elytra in hot Canada balsam containing little or none of the usual solvents. The main tracheal trunks and some of the branches remain clearly visible in such mounts for several hours.

In terms of the system of classification proposed by Comstock and Needham, the usual tracheae present (Figs. 18 and 21, Pl. II) are the costa (*Co*) which branches near its distal end, and subcosta (*S*) which lies close to the costa on the outer edge of elytron; the radius (*R*) and media (*M*) which lie in the medium portion of the elytron; the cubitus (*Cu*) which lies along the suture, and (*A*) the anal rudiment which lies next to the scutellum.

The six trunks common in insects are represented in but two genera (Amblychila and Mantichora), which have rudimentary wings and specialized elytra fastened together in the adult (Shelford, 1915). These trachea are demonstrated in the adult dried elytra without any difficulty. In Omus, which is closely related to Amblychila, the radius and media have disappeared except for rudiments. The cubitus is the principal trachea. With the exception of Omus and Amblychila it is the anal that has degenerated farthest. Collyris was never very satisfactory for study, but it appears that the cubitus is reduced and the anal wanting. In *Platychila pallida* (Shelford, 1911: Fig. 7) the commonest type of tracheation of the family and probably among the most generalized, so far as the first four trachea are concerned, is shown. The anal is much reduced.

The number of small branches and cross connections is large and too variable to be correlated with other specific characters or with color-pattern characters. Figures already published (Shelford, 1915: Figs. 10 to 19) illustrate this fact. The two elytra of an individual show a marked difference. It is evident then that only the main trunks are at all constant. The costal branch at the center the posterior third of the elytron at the beginning of the curve is very characteristic of Cicindela but bears an important relation to color pattern only in some cases.

Figures 2 to 33, plates I to III are selected to show the relation of unpigmented areas to the main tracheal trunks. Figure 2 shows four cross bands which are cut across by the tracheae. Figures 3 and 4 show the same type of pattern but with the cross bands narrower, the middle one broken in the region of the trachea toward the right and with a suggestion of two or three stripes. Figure 5 shows a similar condition but with the spots in the upper right-hand third of the elytron missing. Figure 6 shows a suggestion of seven cross bands as numbered. Figures 8 and 9 are similar but somewhat broken and with some tendency to forming longitudinal stripes between the tracheae. Figure 9, Plate I shows a longitudinal row of spots and figures 10 to 13, Plate II either rows of spots or continuous longitudinal bands between the tracheae. Figures 14 to 21, Plate III show forms that have lost most of their pigment and have retained it only in the lines of the tracheae. Figure 18 shows a form that appears to have double longitudinal lines between the tracheae and has lost the unpigmented areas in the anterior part of the elytron. Figures 16, 20, and 21 show forms that are highly specialized as to the patterns and have lost most of the pigment and the *media* trachea is almost gone. It will be noted that there are many interesting curves and branches that are related to the color pattern.

Figures 23 to 25, plate III show an oblique joining of the markings to form a vitta that is not related to the trachea and is rather rare, constituting an exception to the usual rule.

As a result of this study of the figures it is seen that in the color patterns of the genus Cicindela exists a system of markings that is related to the tracheae, and also is arranged with reference to the cross bands of which there are five, two of which may be divided as to make seven and that these are arranged as follows: There is a cross band in the center of the longest measurement of the elytron. This location is shown to be the same in essentially all of the cases by actual measurement. There is one at the tip and one at the base, with one or two arranged respectively between each of the latter and the middle one. These intermediate bands are most commonly represented as *one* but are some times divided, but in any case its center, or the center of the intervening pigmented area is half-way between the two adjacent, unpigmented more permanent cross bands. It is also evident that there is a possibility of fusion of joining of light areas, so that these lines of fusion are in the spaces between the tracheae and in the region of the cross bands.

The areas near the hairs described in a preceding section are the very last to lose their pigment in the forms that become almost entirely without pigment. It is to be noted that in the forms that have the longitudinal stripes and cross bands broken up, the media is almost entirely gone. It has been shown that these cross bands are the most constant wing markings in insects and are usually represented as the *five* first mentioned. I have gone over very large series of Coleoptera, (Tower, 1906), and find that this is true for this order, while cross bands in the Lepidoptera (Braun, et al. cited), Diptera, Orthoptera, Tricoptera, Plecoptera, Hemiptera, have been discussed by Von Linden, Eimer, et al. In the Lepidoptera (Mayer), however, the line of the veins is the one in which pigment is longest absent, but in the Diptera both living and fossil there is a uniformly denser pigmentation of the veins. Doctor Williston tells me that it is true of the fossil forms, and Doctor C. F. Adams found in the development of the color pattern of some common flies that pigment first appeared along the cross veins and spread from these. In the Hymenoptera the veins are often pigmented and the same is true of the Mecoptera, Plecoptera, some Homoptera, etc. Pigment is usually found in muscle attachments and wherever rigidity is necessary; this has been reported by Tower (1906) in Coleoptera, and in Polistes by Enteman (1905). Since the veins are supporting structures, one would expect that they would usually be pigmented. The great development of the secondary cuticula in the Coleoptera might, since the elytra are no longer used as wings, show modification characterized by the loss of this character in some cases. I find no observations on the secondary cuticula of the wings of Lepidoptera.

In the Ctenostomidae are found bands iu some of all of these positions noted in Cicindela (Figs. 26 and 27, Pl. III, also 376, Pl. XVI.)

In the Collyridae it appears that the band at the base of the elytron (*1*), one in the middle (*4*), and the one at the tip (*7*), are quite common and well developed (one or all). *Collyris celebensis* Chd. (Fig. 28) and *arnoldi* McL., *horsfieldi* McL., *fasciata* Chd. et al. have such bands. In Theratidae are found markings which conform to the cross bands of Cicindela, (Figs. 332 to 337, Pl. XVI), but the areas represented in the two ends of the elytron may be much extended (Figs. 236 and 237, Pl. XIII).

Turning to the other form of the Cicindelidae proper, one finds that in the Euryodini and the Odontochilini markings occur in the same relations to structures as those already described. Among the Euryodini, in Caledonica occur some of these cross bands indicated, and in addition a very interesting thickening of the elytron in the lines of the tracheae (Shelford 1915: Fig. 25). These may or may not correspond to the thickenings that are associated with the veins of other insects, for in the Dromicini, (Cicindelidae proper) we find thickenings that lie between the veins and may be regularly arranged (l. c. Figs. 35 and 36). It will be noted that there are spots in places corresponding to those already mentioned, for example, crossbands in figure 29 representing the Odontochilini, and longitudinal stripes in figure 30 representing the Dromicini.

In the Megacephalidae the color patterns are in some cases like that shown in figures 370-372, plate XVI, which accord with those of Cicindela. In *Megacephala klugi* we find a curious dark spot in the position of the cross veins between the subcosta and the ramus which corresponds to the condition that Tower (1906) has called attention to in the Coleoptera, Lepidoptera, etc., but it is not of frequent enough occurrence to be significant. I know of no color patterns in the Palaeomantichoridae or the Neomantichoridae, both the wings are rudimentary and in the latter the eyes are much reduced and they are in some cases light avoiding.

In *Platychila pallida* we have only a very slight pigmentation anywhere on the body; the wings are reduced to a rudiment that is barely distinguishable and the elytron is pigmented only in a small area lying in its anterior two thirds and along its inner side. There is no development of spaces in the secondary cuticula sufficient to make the chitin opaque and yellow.

In the Dytiscidae, Carabidae, and Haliplidae, the chitinous columns are arranged in definite rows and likewise in many cases the hairs and glands. The center of these chitinous columns, or better the primary cuticula over the chitinous columns, is last to lose its pigment; accordingly one may find a line of pigmented spots lying in rows, often two rows, between the tracheae, for example as is shown in the *Bembidium versicolor* Lec. (Fig. 35). The row of chitinous columns break across the white markings and in some of our common Haliplidae, for example, the chitinous columns are so arranged and the centers are associated with the openings of glands, the cells of which have caused the column to be cut half in two.

To find what are the conditions of the tracheal structures in other Adephaga I made an examination of a number of forms in the Dytiscidae, Carabidae, and Haliplidae, (Figs. 34 to 41, Pl. IV). Omophron shows all six tracheae and three cross bands which do not appear to be related to the tracheae. *Bembidium versicolor* shows only five tracheae, but the unpigmented areas are in the lines of the tracheae and also between them. *Nebria complanata* (Fig. 37, Europe) shows the tracheae in the lines of pigmentation as well as a suggestion of the double banding shown in the Dytiscidae. The Dytiscid (*Hydacticus stagnalis,* Fig. 38) shows all of the six tracheae and a light line both between and directly above them. Figure 39 (*Laccophilus maculosus*) shows suggestions of cross bands and double stripes. *Agabus teniolatus* (Fig. 40) shows the tracheae within the lines of the unpigmented cuticula. *Hydroporus undulatus* (Fig. 39) has the cross bands and the tracheae apparently between the spots. (Compare with figures 2 to 25, plates I to III).

From the studies preceding, especially the last, it is observed that there is no constant relation between the tracheae and the distribution of the makings or unpigmented areas, of such a character as to suggest a direct physiological relation between the two. In the specimens in which the tracheae are unusually arranged there is no effect on the color pattern or variation on that suggests a direct relation between the two. Nor is there any connection between the oxygen supply from the tracheae and the pigment. And as the blood sinuses and tracheae are for the most part coincident, I see no reason for relating the blood supply to these characters. The folding of the elytron in the pupa is apparently not related to the cross bands. It accordingly appears that the relation of pigment formation in the elytron to structure is not directly causal, at the present stage in the evolution of the groups but is one belonging to the general structural organization, hereditary in character.

THE COLOR PATTERN PLAN

The pattern of the Cicindelae is analyzable into the areas or tendencies shown in figures 42 to 49, plate V. Figure 42 shows the full number of dark and light longitudinal stripes. The light stripes are labeled *a*,*A*,*B*.*C* ; *a* is not usually distinct. Very often it is absent as in figures 3, 4, 6, and 11, but sometimes appears to be present without *A* as in figures 5 and 13, plate I and II. It is often present and partially separated from *A* in an Australian species (Figs. 50 and 51, Pl. VI) only. This Australian species is the basis for figure 42. More often it is joined with *A* (Fig. 43), and not recognized separately (Fig. 52). Figure 44 indicates a tendency to double lines between the tracheae suggested by an African species (Fig. 53, also 57 and 7 and 8). Figures 54 and 56 show the longitudinal stripes partially represented.

Figue 45 shows the full number of cross bands rarely complete numbered *1* to *7*; but perhaps best represented in figures 57 and 59 to 63 where they occur broken two spots. Bands *5* and *6* occur nearly complete oftener than *2* and *3* (Figs. 57 and 75). Figure 46 shows the type in which *2* and *3*, and *5* and *6* are fused. This is almost a duplicate of the pattern of an African species, figure 58, but also well represented by figures 73 and 74. Figure 47 shows a common type, cross bands *5* and *6* being separate but the more anterior ones being reduced at the anal side of the elytron. Figure 48 shows all the possible spots which resulted from the superposition of the longitudinal stripes and cross bands. There are 19 of these, of which 11 occur in an Indian species (Fig. 62).

Figure 49 shows the spots or elements from which the characteristic patterns of the group are made up. This pattern should be compared with figures 31 to 33, plate III, which show that individual variations follow the rule of the entire group. The usual pattern of *C. tranque-*

barica Herbst is seen to be made up of *A1, A2, B3* (*humeral lunule*); *A4, B4, B5, C5* (*middle band*); and *A6* and *7* (*apical lunule*). In figure 31 may be noted the forward hook-like extension on the so-called *humeral lunule* which represents *B2*, the union between *B5* and *C6*, etc.

Figures 61 to 72, plate VI indicate some of the commoner combinations of spots. Figure 66 shows a union between the humeral lunule and *A3*; figure 70 a combination of *7*, with *B6* and *B5* which are connected with the central cross band; figure 71 a cross connection in band *2-3* between stripes *A* and *B*; figure 72 a cross connection in band *4* between *A* and *B*; figures 76 to 77, plate VI show the reduction of cross bands to large spots. Thus the conclusion that the patterns are derivable from combination, loss, and extension of a number of inter-tracheal spots falling in cross rows seems justified. There are various types of combination and extension which are not common when the group is considered as a whole, but which represent tendencies in certain isolated groups of species and which must be illustrated (Figs. 78 to 98, Pl. VII) here because they othewise appear to be obstacles to the plan. One of these tendencies is one toward oblique combinations indicated in figure 78 (a diagram). One type indicated by the wide stippled band is shown in figure 79, a South American species. A similar combination occurs as a variation in an Indian species (Fig. 80). A more gentle sweeping combination is shown by the narrow white line in figure 78 and occurs as the regular pattern of an African species (Fig. 81); shorter curves occur in another African species (Fig. 82). Other oblique combinations are shown in figures 83 and 84. The type of obliqueness shown by several African species (Figs. 85 to 87) is an oblique shifting of the entire pattern; it appears to be turned parallel to the end of the elytron. This appears to be a significant tendency and will be discussed again in connection with the discussion of experimental results.

Figures 88 to 91 show a tendency toward obliqueness of markings reversed as compared with that just described and characteristic of the *princeps-cylonensis* group of India and Africa. It may be said to characterize the patterns of a group standing apart from the other representative of the genus.

Figures 92 to 95, plate VII show unusual sinuate extensions of the markings. In figures 92 and 93, Indian and Australian species, a marking resembling the usual "middle band" arises in the area *A2.3* with a form similar to that found in figures 94 and 95. Figure 96 shows bands *5* and *6* separate toward the outer margin of the elytron and united toward the inner. Figure 97 shows unusual extensions of the markings giving two light bands between the tracheae (compare with Fig. 19, Pl. II); 98 shows unusual direction of extension.

From the preceding discussion and diagrams I concluded that even the most complicated patterns are reducable to the usual plan or are made up of unusual combinations of spots occurring in other groups of species. Certain laws regarding direction of shifting of markings seem to prevail. These will be noted again in another part of the paper, (page 58).

COLOR PATTERN AND PIGMENT DEVELOPMENT

As an example of the usual type of pigment development in Cicindela let us follow the events in *C. tranquebarica* (Pl. VIII). In the youngest pupae there is essentially no pigment present except sufficient in the eyes to give a slight brown color. This gradually becomes darker until the end of about ten days when the eyes are a dull brown and the process is apparently complete. At the end of 12 days the tarsal claws, the tip of the mandibles, and the tips of the mandibular teeth have received their full quota of pigment; the pigment proceeds from the tips proximally and by the 13th and 14th day pigmentation is complete. On about the 13th day the distal portion of the tibia of all of the legs show pigmentation on the outer side and this proceeds to the more proximal portions most rapidly on the outside of the leg. The most distal parts of the tibia are pigmented about 2 or 3 days later. Coincident with the development in the tibia is the development in the trochanters where it begins at the outer margin. A slight darkening takes place in the mid-portion of the developing hind wing which is so folded as to make the tip of the pupal wing show dark. At this time, viz., at the end of from 14 to 16 days, the insect emerges. Often at or before the time of emerging the first color centres of the dorsal side of the abdomen have appeared on the last abdominal segment and more rarely also the corresponding centers of the next to the last segment are also present (Fig. 105, Pl. VIII). Usually the animal emerges with the tibia, tarsal claws, part of the trochanters, eyes, mid-portion of the hind wing, and tips of the mandibles pigmented (Figs. 101 and 105*a*).

The later history exclusive of the elytra is as follows: The pigmentation begins first on the distal joint of the antennae and the maxillary palps (Fig. 101), and on the teeth of the maxillae. After about 8 hours the tip of the inner palp and the ligular portion of the labium shows pigment (Fig. 102); next after about 12 hours the distal segment of the labial palp and the outer wings of the labium darken (Fig. 103). The gula begins to show pigment about as soon as the ligula, and the pigmentation of this part is complete at the end of 12 to 15 hours. At the time (after 12 to 15 hours, Figs. 103 and 107) the general pigmentation begins to be most rapid, pigmentation begins to show strikingly at the proximal portion of the appendages just noted and proceeds to meet the distal pigmentation (Zeleny, 1907). The extent to which it goes differs in different species and gives a faint pattern to the parts in some species. The pigmentation which begins distally, usually proceeds only through the extent of the more distal segments (Fig. 109 *a* to *e*). By the end of 24 to 36 hours (Fig. 104) the pigmentation is nearly complete by development over the general areas of both body and appendages. Thus in the antenna at the end of 8 to 10 hours rings appear toward the distal end of the three proximal segments, darken and spread toward the proximal ends of the segments rapidly (compare Figs. 109 *c*, *d*, and *e*). The pattern shown in the antennae, legs, mandibles, palps, etc., persist in some species (see page 24).

At 3 to 6 hours after emergence (Fig. 105*a*) the suture between the clipeus and head becomes pigmented. By the end of 8 hours after emergence there are two oblique color centers between the centers of the eyes; these correspond in position to the oblique depressions that occur in the genus Tetracha. Beside these there is a center close to the posterior side of each eye, one just behind and inside of this, and one in the middle of the frons (Fig. 106). Pigmentation then has proceeded backward on the clipeus, and backward from the suture of the clipeus on the head (Fig. 106). At the end of 12 to 15 hours, the pigment of the clypeus and anterior part of the frons and centers just described has increased and extended backward, giving a pattern as shown in figure 107. This process continues with general suffusion over the head with the pattern still in evidence at the end of 24 to 36 hours (Fig. 108).

After 8 to 10 hours after emergence (Fig. 106) the posterior border of the thorax shows two centers in the depression at the posterior side. Little change takes place on the under side from emergence. By the end of 12 to 15 hours (Fig. 107) the thorax has presented some new centers, a longitudinal stripe occurs near each margin, and there is a narrower one between each of these and the center, and the anterior depression is darker than usual. The end of 24 to 36 hours (Fig. 108) shows the obliteration of the centers mentioned above by the pigmentation of the inter-spaces.

On the ventral side of the abdomen and thorax pigment begins on the outer side of the more posterior segments first and centers appear from behind forward. During the first few hours the pigmentation does not begin on the remainder of the abdomen. The next center to appear is the one in the center of each segment near its anterior side, which appears between the 6th and 10th hour. Just a little later a line appears across the posterior side of the segment and there is an extension of the center one at each side and the coming in of the a loop-like addition outside of the first center. This system of markings is best understood by a comparison with the larval segments (Fig. 99 *a*, *b*, and *aa*). If *a* and *b* joined to give the first marking that appears, *aa* standing out clearly and all of the rest joined laterally, one would have the condition found in the development of the adult color.

No change takes place in the thorax except the development of a center ~~of the~~ on the middle line of the meta-sternum which probably represents the attachment of the large hind wing muscles (Fig. 102), until the coloration of the abdomen is has been completed in the ventral side of the third, fourth, and fifth, and last abdominal segments; this having proceeded from behind forward. At the end, 12 to 15 hours (Fig. 103), it will be noted that the hind coxae, the ante-coxal pieces, the episterna of the metathorax and the coxae of the other segments have received a quantity of pigment and a new center has developed behind each metathoracic leg on the metathoracic sternum. The next stage represented (24 to 36 hours, Fig. 104) shows a general diffuse pigment on the entire ventral surface except the outer sides of the metathoracic coxae which long remain unpigmented. The ante-coxal piece is nearest complete. The great possibilities of being deceived as to position of the color centers is shown by the fact that the abdominal centers and center behind the legs on the metathoracic segments is lost entirely in the last stage of the development.

Conditions on the dorsal side are very simple and centers appear just as in the larvae (Fig. 100) two in number on each segment, begin on the last segment, and move forward fusing in the middle line, and in course of about 10 hours after emergence (Figs. 106 and 107) the color of the dorsal side of the abdomen is practically complete.

In regard to the color centers of the ventral side of the abdomen it may be said that they are the same in number and arrangement as found by Tower on the ventral side of the abdomen of the potato beetle larvae. The abdominal centers are serially homologous. The pattern of the dorsal side of the abdomen of the larvae if Leptinotarsa is similar to that of the ontogenetic ventral of the adult Cicindela. The upper side of the abdomen in the potato beetle larvae is divided with respect to these structures because growth, bulging, and wrinkling due to the extension divide the dorsal side into two parts, and have resulted in the separation of the centers into two rows or bands (see Tower, 1906: Pl. 18). In the larval Cicindelidae, however, it is the ventral side that is extended in the process of the development and which may be wrinkled and the centers are separated just as in the case of the dorsal side of the abdomen in the larvae of Leptinotarsa. There is never any tendency for the dorsal side of the cicindelid abdomen to wrinkle; in fact it is reduced as compared with ventral. On the ventral side of the adult Leptinotarsa abdomen six centers appear but these are not divided as to the middle of the segment. Tower's basipleural is no doubt represented by the three spots that are near the spiracle (Fig. 99, Pl. VII).

In the prothorax of the tiger beetles it is to be noted that the ontogenetic coloration is parallel to that in some of the Leptinotarsae; the two pairs of parallel lines which occur appear to correspond to markings that are on the prothorax of the *C. tranquebarica* (Fig. 107). The two oblique centers of the frons or epicranium in the Cicindelidae are represented in the Leptinotarsae also the two markings by the eyes.

I have noted that in the antennae centers arise in the form of rings around the distal ends of the 2d, 3d, and 4th segments (Fig. 109 *c*, *d*, *e*.). Conditions in figure 109*d* and *e* show patterns in the development of these which are the exact duplicate of the patterns in the antennae of the *C. strachani* (Africa) which has also a primitive elytral pattern, *C. theratoides* (New Guinea), many of the Megacephalidae and some Collyridae.

The development of the pigment in the legs up to the time of emergence is described above; after emergence the development proceeds from proximal to distal in the tibia and in the same succession in the tarsal segments. Previous to emergence the humerus is somewhat compressed and wrinkled, being only about two-thirds as long as after the expansion which follows emergence. At the end of about 8 hours one finds the femor beginning to show a general suffuse pigment which appears to arise simultaneously over the entire surface. After this the later history in the legs in simply a general intensification of the pigmentation.

In all of the species of Cicindela studied the phenomena of pigment development are the same so far as has been noted above with the exception of the *punctulata* and *lepida* in which the first centers appear in the middle of the ventral side in the third and fourth abdominal segments. This is the case in *T. carolina* in which the centers are like those in the larvae. The adult abdomen in this species is not pigmented toward the posterior end of the ventral side while the upper side never receives any pigment at all and the usual larval color center are, as has been stated, very much reduced in this species. Likewise the centers of the head and prothorax are little developed and the oblique ones near the center of the frons are very faint. The two which appear first in the posterior depression of the prothorax are quite distinct and very suggestive of the condition in the *Megacephala* (*Phaeoxantha*) *klugi*. The legs are, however, not pigmented at all and it appears that the cuticula in these cases is of the type with interlamellar spaces which is a means of giving strength to the less rigid parts of the body.

An examination of stained whole mounts of the appendages shows that as a rule the distal portions are first clearly differentiated and first to take on the form that the part is to have in the adult. The tip of the mandible is the first to show the distinct pointed form toward the head, tooth after tooth being differentiated from the somewhat larger mass of tissue which makes up the mandibular outgrowth. The same is true of the other mouth appendages, labrum etc., they become more hairy in form and stand well separated from the old pupal skin. In the case of the leg the tarsal claws are the first differentiated and this process appears to move in a general way toward the body, segment by segment, the femor being last to be differentiated and last to receive the pigment. The position of the pigmentation in the tibia corresponds to the point of attachment of the flexor of the tarsi. This is early developed and thus the tarsi are the first to become movable; at this time the flexor and extensor of the tibia are not well developed, their muscle striations appearing indistinct, but become much more distinct and definite in form a little later and the tibia becomes movable about the time of this development of its pigment. A similar development occurs on the proximal portions of the trochanters which are the attachment of the muscles. The wrinkled condition of the femora helps to give it rigidity and the legs are well enough developed to allow of sufficient movement to release the animal from the pupal skin. The legs are at first somewhat extended and subject to a considerable amount of movement, and while the body is flexed and extended and the pupal skin ruptured in the midline of the thorax the mandibles are then worked as well as the other mouth parts and the head removed by repeatedly throwing it backward. The animal gradually wriggles out of its skin and the wings and elytra soon expand; the wings expand to the full length inside of about 20 minutes after the animal emerges, and remain thus for several hours. If for any reason the expansion of the wings or elytra is interferred with, they always remain in the exact condition in which they were placed by the adverse conditions, and if the wings are not folded in the normal fashion at the proper time, they will always remain completely extended. Their early pigmentation, if it is associated with hardening, is probably an advantage to this process of withdrawal or folding.

It seems altogether probable that the peculiar manner of development of the pigment is associated with the development of the structures which are necessary to ectosis and that they accordingly represent developmental adaptations. In the case of the tiger beetles which do not have the appendages pigmented in the adult the cuticula must harden without being pigmented.

The animals emerge with the elytra entirely unpigmented and during the first 4 to 8 hours little change is easily noted. One can hardly record the beginnings of the pigmentation as this is very faint, and the wings beneath, which come between the elytron and a part of the pigmented abdomen, give no opportunity for accurate observations with the elytra in position except as one slips pieces of paper under them, which may injure the elytra so as to give abnormal development. The elytra must be removed and mounted in glycerine jelly, or cleared in balsam. It is necessary to hold the slide in position over the surface of a good glass plate that has been painted white on the lower surface and not magnify them or if so, only about two diameters with a reading glass. The fresh, unmounted elytra may be placed in formalin in a watch glass painted a neutral gray or yellowish tone which is the same color as that presented by the elytron before pigmentation when viewed in transmitted light. By this method and with individuals killed at different stages, and with the use of a Zeiss binocular microscope, I have been able to follow the course of pigmentation of the elytra. The elytra have been examined in cross section; there are no thickenings in the primary cuticula in which all the pigment is located, except the small thickenings that have been described as occurring in the area immediately in front of hairs, and these have been carefully considered and their relative number as effecting the color effect practically eliminated. The cuticula is somewhat thinner at the tip of the elytron. The actual hairs present are surrounded by an area that is fully pigmented, but this also has been taken into account. Elytra of *C. repanda* show beginnings of pigmentation which often are strongest near the costal border at the end of 4 to 5 hours (Fig. 111). The chief of the areas showing lack of pigment are in the lines *A* and *B* and are particularly prominent near the base. Later (Figs. 112 and 113) these lines are broken into spots which correspond to spots found in certain Eurasian and African species (Figs. 147 to 187, Pl. XII, and 241 to 280, Plate XIV). The series of stages that I have had has been small and not suited to the detailed comparison as some of the following species are, but shows the same thing.

The color development in *C. lecontei* Hald. begins very faintly apparently at about the posterior end of the anterior third of the elytron at first the permanent markings are difficult to distinguish, but a little later they become distinct patches. Two ontogenetic markings between the base of the elytron and the general arrangement of pigment at the end of 4 to 5 hours (Fig. 114) correspond very closely to conditions found in *repanda*. Longitudinal, heavily pigmented stripes that stand out in some individuals, lie in the lines of the tracheae and hairs, and become more pronounced as the development continues. Figure 115. 12 hours after emergence, shows none of the spots characteristic of the others shown but has indications of a cross band which never occurs in *lecontei* but which is present in *rugifrons* and *modesta* of the Atlantic coast. Figures 116, 117, 118 show a number of spots arranged in longitudinal rows. A comparison of these with figures 156 to 177 and 244 to 261 will make clear a close correspondence between the spots appearing and those in adults of Eurasian and African species. Pigment fails to develop when the elytron is wet (Gortner, 1911). This happened in practically all wet elytra of this species and very few of those in other species.

Development of pigment in the hind wings begins a little back from the anterior end, and in this case, about the time of emergence (Fig. 119), in the region in which the folding occurs, and shows while the wing is in the pupal skin thus causing the tip of the pupal wing to look black. Pigment passes out along the veins in both directions and vein after vein is pigmented toward the anal border. This process requires several days for completion. Figures 119 to 122 show the wing from the time of emergence to the end of about 24 to 36 hours and the adult.

Development in *C. purpurea* Oliv. var. *limbalis* Klg. (Pl. X) perhaps shows more definite spots than any of the others. The first evidences of the pigmentation in ontogeny is in the small circles around the hairs on the elytron; this takes place about 3 hours (Fig. 123) after emergence.

At the end of 8 hours the pigment usually begins to come in generally, first, in the lines of the tracheae. As in the case of the lecontei the first trace is at the posterior end of the anterior third of the elytron. The principal early developmental markings show as large light areas (Figs. 124 and 125, after 8 to 10 hours) which seem divided again later (Figs. 126 to 129, Pl. X) and correspond to the spots found in old world species, figures of which have already been cited. Heavier pigmentation often persists in the line of the tracheae even in the adult (Fig. 130).

In *C. tranquebarica* (Pl. X) the pigment begins first a little behind the anterior end, as in the other species, and comes in the lines of the tracheae with all of the bands represented and the spots growing smaller and the longitudinal stripes less and less prominent as time goes on. In all the elytra, however, the same markings appear as in the other species (Figs. 131 to 134), and spots occurring in other species are consistent in occurrence.

C. punctulata (Pl. XI) begins pigmentation about 4 to 6 hours after emergence and the pigment appears to pass from the anterior to the posterior end of the elytron. Certain lighter areas appear especially at the base of the elytron and between the tracheae, figures 135 to 137. These represent cross bands and other bands occur further back appearing in some cases but all are comparatively indistinct. There is, however, a different phenomenon such as occurs in some of the Dytiscidae,

e. g., *Laccophilus maculosus* (Fig. 39, Pl. IV), a concentration of the pigment around the markings. Even where the markings are absent or almost so the denser pigmentation is present. This seems to have obliterated ontogenetic markings as they are shown less plainly in these species than any other studied. Such spots occur in some species of Cicindela as for example *campestris, aulica polysita, latreillei* (Fig. 257, Pl. XIV) and *ismenia* (Fig. 366, Pl. XVI), which have a more densely pigmented spot in the region of the sutural spots of other species, i. e., in the position of *C2.3* (Fig. 48, Pl. V). In cleared elytra of *campestris* a dark area appears at this point. Elytra of *C. limbalis* (Fig. 127, Pl. X) shows this. In some cases dark spots appear at this point in surface view; in others metallic spots. When the dark color occurs, the conditions described in page 51 are reversed—the surface film is absent. The distribution of the chitinous columns above which areas are first pigmented makes the study very difficult. The hairs on the elytron which lie in the lines of the tracheae show pigment around their bases by the end of 3 or 4 hours if not earlier. The elytron reaches the adult color so far as pattern is concerned at the end of about 15 hours, but pigment continues to be deposited for several days.

Only one stage of *C. sexguttata* (Fig. 138) studied shows the spots in the area between the tracheae faintly. The pigment is piled up about the markings only to a slight degree. *C. punctulata* and *sexguttata* belong to one of the Mexican groups and differ from the other species studied.

One specimen of *Tetracha carolina* (Fig. 139, Pl. XI) was studied; in this the pigment began to develop at the end of about 9 hours and to manifest itself at the outer side of the elytron where it bends under, and appears to move toward all parts of the elytron from there. A somewhat lighter streak was left, however, between the costa and the subcosta tracheae; this corresponds to stripe *a*, figure 139. The pigment moves toward the inner angle but shows a lighter space at the base between the ramus and the media and also a longitudinal stripe between the media and the cubitus, which is broken at a point corresponding with the dark band *B* between *2.3* and *4*. This same break occurs in the area between costa and subcosta. That portion of the tip of the elytron between the media and the suture is the last to be pigmented. Figure 140, which represents the elytron at the end of 9 hours shows adult coloration. The darker dots represent the chitinous columns over the center of which the primary pigmented cuticula is thicker than any where else. At the point where it has been stated that the pigment began developing the citicula is somewhat thicker than elsewhere.

In *C. hirticollis* (Figs. 141 to 145) the pigment appears to begin almost uniformly over the elytron except for the weaker places representing the ontogenetic markings. The lighter places are between the lines of the tracheae. There are cross bands at the base of the elytron, the middle one usually more or less clearly connected with the distal end of the adult cross band *3*. Usually there is a spot opposite the end of this band between the media and the cubitus and usually another set of dots stretches across the elytron between the band *2* and band *4*. These bands of a secondary nature are not present in the later stages or if so not marked. The longitudinal lines become weaker as time goes on and the markings, except those that are to be permanent, gradually disappear; those in the region of the base are last to go. In some cases lighter longitudinal lines are divided into spots.

A late stage in *C. 12 guttata* shows the same longitudinal stripes and cross bands. Throughout the series *longitudinal stripes* seem to be most marked in the earlier stages but become partially divided later and are rarely or never continuous but nearly always broken into spots. This is shown in nearly all the figures presented and the conclusion which seems warranted is that the longitudinal stripes are a more definite character than the cross band, though neither occurs alone. The fact of a combined cross and longitudinal system of unpigmented areas is the one which comes forcefully forward in the entire study though there are irregularities present. Further, one sees a close resemblance between the ontogenetic patterns and those of the African and Eurasian species on which the analysis of the pattern was based. One notes also the close correspondence between the spots shown in the general plan presented in figure 48, plate V, and those occurring in the ontogeny of the patterns of common North American species. This would seem to establish the plan of the pattern as well as could be hoped.

The entire set of evidence presented tends to show that the simplest type of pattern in the Cicindelas is a pattern of spots lying in lines between the chief longitudinal tracheal trunks and falling into cross bands of which there may be seven. In ontogeny these are subject to some variations but such a description fits the general relations found better than anything else that can be stated. Such a type of pattern, which is of the character that is commonly called primitive, is what might be expected among insects. The wings are usually characterized by longitudinal veins which are thickened and hardened and often pigmented. These veins are connected transversly by cross veins which are much more diversified in the insect group than are the longitudinal ones and which are also much more subject to individual variation. Tracheae usually occupy the longitudinal veins but not always the cross veins, hence in the insects which have actual cross veins there is not a necessary correlation between the veins and the tracheae. The greater hardening and more general pigmentation of the veins of many insects already mentioned (page 16) leads to a spotted type of wing, in many cases at least. Such a system offered in the elytra of the tiger beetles gives the basis for the spotted type of elytron which we find frequently in the group. Veins no longer occur definitely longitudinally and the tracheae do not ordinarily bear any definite relation to cross areas.

A large background of evidence is presented above for the selection of the spotted type of tiger beetle pattern, made up of spots falling into rows and forming stripes and rows forming cross bands, as a general one from which other types are derivable *by the loss of spots, combination of spots,* etc. Comparable analyses were presented by Eimer (1895) and Von Linden (1902), who note cross bands as the basis of the patterns of various species of Lepidoptera. Tower (1906) reduced the general plan of markings in Leptinotarsa to cross bands and longitudinal stripes. He recognized 4 or 5 unpigmented cross bands and 6 longitudinal unpigmented stripes which fall in the lines with the tracheae instead of between them as in in Cicindelidae. He shows the stripes divided into two in the area between the costal and subcostal tracheae (Tower, 1906:228, Figs. 5 to 8, Pl. XXIV), which is comparable to the condition suggested in the carabids and dytiscids shown in figures 35, 38, 39, and 40, plate IV. Tower adhered to a theory often held by embryologists, namely that the base of the wing is oldest; further, that pigment appears first in the base of the elytron and proceeds to the distal portion in accord with the relative age. No conclusive evidence is brought forward to show that the base of the elytron is actually oldest, and an examination of Tower's figures (Tower, 1906: 156, Figs. 1 and 2, 7 and 8, Pl. 19) shows that the basal part of the elytron in some species is not first pigmented. Pigment begins in the costal border of the wing and at the level of the second dark cross band which he calls the "proximal" and which is very common in his group. This is comparable to the early stages in Cicindela (Fig. 111). The view that pigment comes in first in cuticula over the oldest tissues from the embryonic standpoint seems not to hold good in Cicindela, for on this basis certain abdominal sclerites would be embryonicly older than others (Figs. 102 to 104, Pl. VIII), the last abdominal segment older than the first, and the femur younger than the tibia as well as other peculiarities shown in figures 99 to 103. The law cannot be said to hold good at all in the group under consideration, but rather as has been noted on page 24, there is an order of post embryonic development of adult organs, which coincides with pigmentation.

One of the most recent color-pattern analyses (Braun, 1914) shows the pattern of Lithocoletes (microlepidoptera) to be made up of a modication of seven transverse dark bands with six transverse light bands between them (page 161). The figure of the hypothetical pattern is in general terms almost identical with that shown for Cicindela and independently conceived on plate I, figure 4. In this second and third light band are represented by a single wide one and the fifth and sixth are separate as two narrower bands. If the general plan of longitudinal and cross bands in insect patterns is to be accepted we must also conclude from the evidence presented that the relations to trachea may be reversed, i. e., the pigmented areas may lie immediately above the tracheae or between them. In the Lepidoptera pigment appears last in the veins (Mayer, 1896).

The areas between the trachea may be subdivided into two longitudinal bands. The pigmented and unpigmented bands may also be reversed in position as would appear to be the case when we compare the usual cicindelid patterns with those studied by Tower. There is no reason why this should not be the case as when markings are lost; the pigmentation which results is often heavier than elsewhere (Figs. 135 and 136).

However when one compares the cicindelid ontogeny with the existing patterns of other orders one finds that they show a series of light spots such as might easily correspond to the so-called cells or areas divided by longitudinal and cross veins in a primitive insect such as a may-fly. The may-flies, stone flies and many diptera show such an arrangement in some parts of the wing. At least it may be safely concluded that a pattern of faint spots is the primitive type in Cicindelidae if one accepts any of the current criteria for primitive forms.

I start with this type of pattern as "primitive" with a consciousness of the fact that it would be possible to proceed in entirely different directions and from entirely different starting points and make out cases of modification in definite direction fully as plausible as the ones here presented, provided only the preceding strong evidence is not accepted.

On this account it may be well to give the reasons for presenting this matter of modification at all. First, it is presented to further establish the contentions already made as to the character of the pattern plan presented; secondly, to show that all even the most specialized types of patterns could have been derived from the generalized types described above; thirdly, to show that there are certain laws of modification which must have been very general in the group and which have operated again and again in the production of the characteristic types of patterns.

Figures 149*b*, 156*a*, and 165, plate XII, show some of the patterns in which five nearly complete cross bands occur; 179 shows a very simple band, *1* with a complete, *4* etc.; 185 shows a wide cross band representing *3* and *4*. Figures 149*b*, 149*a* and 156 represent the patterns of an African species showing that variations are in the direction of greater obliquity of the cross markings, 149 approaching very closely to 148, which is a different species and usually oblique. A third species is strikingly oblique but still possessing the usual cross bars of the group of species. Thus in this small group the usual typical pattern as shown by the general observations preceding is decidedly distorted by in a definite direction.

In figure 165 is shown a type of pattern in which the cross bands are nearly vertical to the inner line of the elytron; all the spots present fall in to such bands as they do in the ontogeny series (Figs. 112, 113, 116 and 117, Pl. IX; 128 and 133, Pl. X; 143 to 146, Pl. XI). In all the other figures on the upper half of the page the two spots near the elytral suture are not in line with the cross bands. Evidence of this will also be found in the ontogeny series but is less marked than the tendency toward transverse bands. In 165 and 165*a* and in 156 and 156*a*, plate XII, the components of crooked middle band are clearly brought out in course of variations in which two bands may or may not be joined in the stripe between the media and radius. This tendency should be noted as the most characteristic of the genus Cicindela, as there is scarcely a group of species as arranged on the basis of pilosity by W. Horn in which some one does not show this type of joining. The breaking of the cross bands by pigment in the line of the media is also very characteristic, but the tendency for the spots to lie out of the lines with the cross bands as interpreted, is taken as evidence of one of the general tendencies to be discussed later. The relations of the characteristic patterns to the general plan is thus made evident. Another general tendency also manifested is the tendency for the spots shown in figure 156*a* to spread and join, not in any direction but in definite lines. The figures to the right and above figure 165 illustrate the tendency for the markings to join in the line between the pigmented areas of the media and cubitus and for the individual markings to still retain their characteristic form. On this basis the unusual and aberrant patterns such as 150, 151, 152 and 160, 161, 167, plate XII, are easily explained. In spite of the extreme extension they are like 157.

Figures 170 to 187, plate XII, show the patterns of species in which the longitudinal striping has been developed chiefly in conjunction with some cross bands, but in which there is no suggestion of the characteristic middle band. Figure 169*a* shows the pattern of an Australian species in which all the dark and light longitudinal stripes are represented. The dark area over the subcosta is clearly distinguishable. In 169*a* this subcostal dark stripe is reduced but still present.

Figure 169 shows the extreme extension of the white; 168 shows a reduced pattern of the same type; 175, a species with three represented simple stripes; while 183 has only one stripe; 170 and 170*a* show the variation in one species in which the middle white stripe may be either present or absent, and the two posterior cross bands are present and curved like the end of the elytron. In 171 the cross band is broken away from the innermost longitudinal stripe in the area of the dark line of the media trachea; 172 shows a wide middle band with the longitudinal stripe represented only in the anterior portion. Figures 173 and 174 show types with connections between an outer, unpigmented side and the central light stripe in the center. Figures 177, 178, and 171 show a combination of the lateral stripe and the cross band *5.6*: 180 to 181*a* show patterns which may have arisen from types like figure 158 above. Comparing 177, 182, 184, 184*a*, and 176, one notes varying lines of oblique connection to which attention was called in figures 78 to 87, plate VII. Figures 188 to 231, plate XIII, show cross bands in the Indian-African-Australian group in which reversed obliqueness of the central band *4* is developed. This obliqueness is rare outside this group except in forms with a well developed sinuate middle band (e. g. Figs. 292 to 298, Pl. XV). Figures 188 and 188*a* show the well developed cross bands, *1* and *2.3* being joined at the side; 189 is similar and *1* and *2.3* are joined obliquely; 190 is similar but reduced. 198 and 199 are similar to 188 but have lost the last cross band and further reduction in the same direction would result in patterns like 197, 205, and 206. 191 to 196 show a series based on the central white stripe variously broken into spots representing cross bands. 200 to 204*a* and 213, plate XIII, are a series of related species occurring in India which show an unusual oblique arrangement and combination. 209 an African species belongs to a group with pilosity similar and closely related to the Indian group including 201 to 204*a*; it shows the same type of obliqueness in the central marking as in 200. 210 to 212, plate XIII, show further modification of the central band and connection with the oblique humeral curve in the line of the central light space. 220 shows a slightly different trend of similar elements which give the combination in 221 or 220 and 219, depending on the trend taken. 214 to 218 and 222 to 231 show the simple patterns of cross bands in which the last and usually the first are missing. 232 to 240 show combinations of markings resembling those just noted in Cicindela, in Therates, Prothyma and Odontochila; compare 232 and 197, plate XIII; 233 and 206, 234 and 197; 235 and 219; 236 and 219; 237 and 188; 238 and 239 with 210 and 213; and 240 with 188. There are resemblances between patterns in other genera and those in Cicindela.

One note-worthy African species (Pl. XIV, Fig. 242—compare with 209, *C. oscari*) shows the unusual oblique bending of marking which characterized the group noted above. This and *oscari* are however the only species in which it occurs and the group to which it belongs is similar in pilosity to the Indian groups just described. This particular one stands in closest relation to those shown in plate XII, figures 170, 170*a*, and 171. It is introduced here because at the *outer margin* its markings represent *2*, *5*, and *6* with the almost universal central or fourth absent, except at the innerside where *4* seems to be present and obliquely joined to *5*. 241, *a* and *b* show a pattern in which *5* and *6* are present while *4* is wanting except for a few small dots. This species appears to show a tendency to double longitudinal lines. 243 shows a second African species in which there is a tendency to double stripes but the central cross band represented at the margin. The patterns show in figures 244, 244*a*, 245 and plate XIV are of especial interest because the division of the second cross band in those numbered *3* and *4* in the preceding figures are both represented as spots. This is of rare occurrence, the more usual arrangement being like that shown in figure 251. Figures 248 *a* and *b* show the double longitudinal stripes of an African species, a case similar to those illustrated above in which one of the types of variation is in the direction of the spreading of the white. Figures 247 and 247*a* show the joining of such markings as occur in 246 and 259 to make a central longitudinal stripe.

Figures 257 to 261, plate XIV, show unusual patterns of spots, which fall into the usual cross bands on the whole, but those in the inner margin of the elytron are usually shifted out of line. Figures 262 to 280 show various directions of reduction of markings in patterns of the type shown in figures 266, 274 and 274*a*. Those at the left show the loss of the central stripe and those to the right the loss of the inner markings, entirely or in part. 281, 282, 283 show the extensions and obliquity in the type pattern shown.

Plate XVI, figures 292 to 306, show the American species in which cross bands *5* and *6* are separated as seen in 289, 294, 293, etc. The general tendency is for the markings to disappear from the anterior to the posterior end.

The component parts of the oblique vitta of some species of the Mexican group is illustrated by figures 311 to 313 and 319 and similar components making a somewhat different vitta in 291, 296*a*, and 297. Figures 315 to 328 show patterns in which the last or apical (*7*) cross band is missing or in which variations arise in which it is reduced.

Figures 329 to 355, plate XVI, show the species chiefly Eurasian, a few American, in which bands *5* and *6* are present and separate, the former illustrated by a marginal spot behind the center. Figure 347 shows a narrow longitudinal stripe extending forward from the spot near the apex, this is an unusual variation in a race of a European species. Figures 361 to 363 show a tendency in certain species for the formation of a vitta in the space between the subcostal and radius (tracheae). Figure 364 shows an unusual joining of the marking of a specimen of *C. limbalis* loaned by Professor H. F. Wickman, in the space between the subcosta and the radius, though the species rarely has the markings joined and when so not in this line (*A*) but in line *a*. 365 shows an aberrant marking in the central part of the elytron of *C. campestris*, which is a common European species. 366 shows the darker spots about the white marking in a closely related species. 370 to 377 show the patterns of other genera; compare 370 and 362; 371, and 185; 372 with 367; 373 with 367.

Figures 402 to 478 are presented to show series of unusual combinations illustrated by the Indo-Australian group of species. 378 shows a marking projecting backward composed of the band *2.3* and the longitudinal part of the pattern plan which lies between the media and the cubitus (tracheae); the lettered number of the same species shows the extinction of the white. 386 shows an unusual type of pattern in which the curve appears to rise in cross-band *3* while the light stripe between the media and cubitus is obliquely joined in the anterior end to the central spot at the elytral base. Extension of the white is common in variations in this group (383, 384, 385), 379 to 382 show a combination between the middle band and the central basal spot and spreading of the white. 389 shows a similar pattern but with the joining in the cross-band *2.3* and extension of the white. 387 and 396 are somewhat generalized, representative of the type in question which with slight modifications may have led to the 397 and 398 series of patterns (*f*) or by extension to the 392-395*a* series and 400. The balance of the illustrations show the unusual patterns of the Cicindelas both reduced to a single marginal stripe and in full form. Most of the species represented are from Australia and New Zealand.

Figures 422 to 454, plate XVIII, show the unusual marking of Cicindelas with slight distortions, but all the patterns belonging to groups of species which show a strong tendency in the chief representatives to vary in the direction of nearly all white individuals. The irregular and oblique marking in figures 422 and 423, representing two South American species, shows an unusual type of degeneration of the system. The peculiar irregular, branched and scattered character of the markings of several groups shown indicates the breaking up of the system of marking which has been designated as the type upon which they are based.

The different species are characterized by peculiar turns forward of certain markings. Compare for example the anterior cross-band (humeral lunule) of 436 and 427; one is turned forward with a characteristic curve, the other backward. This is a difference between the two species which holds good throughout all the individuals. The extension of the white shown is clearly associated with a degeneration of some of the chief tracheal trunks.

From this large series of figures we must not permit ourselves to judge that all types of pattern are equally common and equally general in the species of the genus. Figures 329 to 333, and figures 130 and 131 show the commonest and most characteristic types in the genus which are universally distributed and make up vast majority of the grand total for the world.

This, the first definitely directed tendency in the group, has been the union of spots to form the characteristic markings of the group shown in figure 49, plate V, as combination of *A1, A2, B2*, or *B3* to make the *humeral lunule* so called, of *A4, B4*, and *B5* to make the so-called *middle band*, and of *A6* and*7* to make the apical lunule of the taxonomists of the group. If these three types of joining are granted as the first directive principle entering into the make up of the patterns of the group it must also be noted that it does *not* apply to the majority of species in nine of Horn's groups (XXVII-XXXVI) including 40 species (Figs. 188 to 215 and 220 to 231, Pl. XIII). A few patterns with middle band and apical and humeral lunules, and which have three spots in the basal and anal portion of the elytron, are included in these groups and differ from most others of similar components in the *presence of these spots* (Figs. 273 and 274, Pl. XIV, and 163 and 164, Pl. XII). These few are the only representatives which show this characteristic middle band humeral and apical lunule. It applies to only 16 species of the Horn's pilosity groups XVIII to XXII which include 66 species in Africa (Figs. 147 to 149*a*, Pl. XII; 269, Pl. XIV; 156, Pl. XII; 265, 241 to 272, 278 to 280, Pl. XIV). Of the figures cited, 156 and 265 are of the most primitive type and 266, 267, 275 and 278 show modifications.

If we grant the majority of the remaining 500 species show these characteristics as variations or that they may for purposes of discussions be assumed to have been derived from forms which did have the three characteristic markings we note that in general the patterns except those mentioned above fall into two parallel series one without the spots, including the majority of species, and the other with them, including a comparatively small number of species. Those with the three spots are confined chiefly to the land directly bordering the Indian Ocean being especially numerous in Africa and India. Spots may be wanting in some variants of such species as *escheri* (Figs. 267 and 268) and *monteiroi* (Figs. 276 and 277). These belong to groups which normally have them, but they almost never occur in groups which do not show them in a majority of members. Considering the components of the three spots, the anterior central spot (*B1*, Fig. 49, Pl. V) is a part of the basal cross band *1* clearly shown in figure 179. The anterior one in stripe *C*, figure 48, plate V, appears to be a fusion of spots *C1* and *C2* and the posterior one of *C3* and *C4* as a rule, though sometimes the posterior one is *C4* and the anterior one *C1.2*, figure 165. There is a tendency indicated by variation to drop out these markings in many species. In *flexuosa* usually *C 1.2*, i. e., the basal sutural spot, is first to go. In others this is not true as a rule, as shown in 261, 276, 277 and 280. On the other hand there is no species in which these are present and other markings absent. These facts indicate that these spots show a tendency to disappear first, leaving the types of pattern without them. More rarely they may unite to form a band which may persist in the extremely modified forms, figures 151, 160, and 167. One of the characteristic types of marking which seems to belong to almost the entire group showing the typical middle band, is the oblique shifting of the cross band which makes the *humeral lunule*.

The tendency toward obliqueness of the middle band of the typical forms seems quite general in many groups but by no means universal, and is shown by some species in all the groups, and hence is illustrated in all the groups of figures: 157, 163, 222, 227, 273, 276, 288, 299, 451, 335, 336, 342, 411, and 417.

In other groups another tendency seems to be present, namely toward a sharp forward-bent angle on the middle band (Fig. 482) figures 209, 206, and many others in which the usual combinations have not been affected are shown in plate XIII. On the other hand scarcely a species in plate XII shows this tendency except figure 150. Figures 292 and 293, plate XV, 339, plate XVI, and others related show the same tendency. It is shown in the patterns of the Australian group (Figs. 394 to 396, Pl. XVII) where a middle band involving different elements occurs, and is particularly conspicuous and characteristic in some of the Mexican and South American species (Figs. 428 to 434, Pl. XVIII) where it is the chief distinguishing feature. In the group as a whole the most striking tendency is for the markings to disappear, beginning in the proximal anal region of the elytron and usually leaving the more posterior distal markings present. But to this there are many exceptions in which the central marking on the elytron is the only one left. (See figures 255, plate XIV; 222 to 231, plate XIII; and 206.)

Another tendency manifested in many species is the extension of the white; it is seen to crop out in all groups from any starting point which is in existence and to proceed from the spots characteristic of the group, in the direction of general concentric extension in which the original type of pattern may be recognized (Figs. 160, 167, 169, and 181, Pl. XII; 204, 204*a*, 196, Pl. XIII; 378 to 437, Pls. XVII and XVIII).

Thus one who inspects the figures as arranged is impressed with the fact that there are a great many directions in which patterns have been modified and these figures are numerous and intentionally substituted for less satisfactory descriptions. The material afforded by the 600 or more species is rich in possibilities and excels in this respect the butterflies of Eimer or pigeons of Whitman.

EXPERIMENTAL MODIFICATION OF PATTERNS

To test the laws of modification of the typical patterns of Cicindela larvae of several species—*C. tranquebarica, repanda, hirticollis, limbalis, lepida,* and *lecontei*—were subjected to low temperature, high temperature, and moist and dry conditions. The temperature was raised about 10 degrees C. above that encountered in the normal outdoor life history. The experiments were carried on in the apparatus shown in figure 455, plate XXIX, and described in connection therewith.

The larvae were put into the high-temperature (near 37°, 1906; 40°C, 1905) about May 15. They were placed in a lamp chimney containing fine sand. The apparatus as arranged gave 2° to 4°C. higher temperature at the top than at the bottom. The average of the two was used in computing the mean. Temperatures were taken twice a day as a rule. The temperature rose each day as the sun shone on the cases so that during the hottest weather daily maxima in soil temperature went to 40 to 42 degrees at times.

The results of the experiments on *C. tranquebarica* so far as the patterns are concerned are shown in figure 456 *a* to *g*, plate XX, and 457 *a* to *b*, 458, 459 and 460; these should be compared with control 456 a' to b', w', 457 a' to e', w' and 458 $a'b'$. A comparison of these experiments with their control and the representative of the forms collected in the field from the same generation shows that in the controls the normal middle band reaches to the margin of the elytron where it is expended in the line of the longitudinal band *aA*; the longitudinal part is parallel with the anal side of the elytron; the middle band is hooked at the end or turns into a horizontal position in compliance with the normal direction of the transverse band from which it is derived. The humeral lunule is usually hooked. The angle in the middle band is a right angle and there is a forward extension of the middle band at the angle.

The patterns which result from the experimental conditions almost without exception differ from the control in the following respects:

1. The humeral lunule is usually without any enlargement at the end suggesting an expansion in the place of spot *B2* and *3*.

2. The middle band is withdrawn from the margin in all cases and in only one case, figure 556 *g*, is there any longitudinal extension.

3. The angle of the middle band is always less acute and the forward extension less pronounced.

4. The longitudinal portion of the middle band is oblique to the anal or inner margin (suture) of the elytron.

5. The end of the middle band is not hooked but rounded, and rarely even parallel with the transverse bands.

A close examination of the marking of the experimental individuals show that there is correlation in all the respects in which the middle band is modified, in general the most oblique middle band is almost withdrawn from the margin and shows least hook at the end.

Figure 461 shows an unusual type of marking and of modification, the most reduced marking in specimens of C. *limbalis* subjected to the same experimental conditions as the *tranquebarica* shown above. The usual type of modification which is quite general in experimental specimens has the longitudinal portion of the middle band shortened. It is also more oblique and thus less like the simple type. The middle bands of these specimens approach those of the variety *splendida* (Kansas). They represent a more extreme modification of the simple type than the experimental middle bands of specimens of *C. tranquebarica*. The markings in two out of about twenty individuals (Fig. 461) surviving the high temperature showed a sharp bend forward. This is the reverse of the usual tendency in the *purpurea* group but is a strong tendency in some other species shown in plates XIII and XV. One individual out of several hundred collected from the habitat in question, reared as controls, and reared for ontogeny showed this character. Apparently the tendency to respond by a sharp forward bend is little developed in *purpurea*.

Figure 463 *a* to *d*, 464 *a* to *c*, and 466 show the patterns resulting from the high temperature experiment with *C. lecontei* while 466 *a'* to *c'* and 467 *w'*, *x'*, *y'*, and *z'* show the control which survived and the range of variation in a series of specimens collected from the same area from which the larvae for the experiments were obtained. First of all the high temperature experiments show patterns with reduced markings. The markings shown in 463*a* are joined in a way which rarely or never occurs in the stock from which they were collected and which is on the other hand characteristic of the varieties of this species which occur on the Atlantic coast. Also 463*d* shows a pattern which is smaller in markings than any that have ever been collected near Chicago.

467 *y* representing the smallest, which makes the marking of 463 undoubtedly reduced by experimental condition.

Figures 465 *a* to *b* show experiments in which the larvae, pupae were iced from the beginning of the pupal stage; all either by remarkable accident or through the effects of the experimental conditions show the widest type of markings; a third specimen was only slightly modified. In 465*b* the form of the end of the elytron is rounded in an unusual way and the surface appearance of the entire body and the elytron are different from the normal types.

Figure 468*a* and w′ show the type of modification occurring in experiments on *C. hirticollis.* The middle band is modified as follows: the hooks and angles are rounded, the transverse part which usually turns forward and has a sharp angle as in 468 w′ is oblique in the opposite direction. These modified patterns are identical with those in southern and western localities. This modification is of the same kind as that in *C. tranquebarica* and *C. purpurea.*

Thus it is evident that *C. tranquebarica, hirticollis,* and *lecontei* may be modified in structure and pattern by high temperature during the pupal and prepupal stages. Experiments performed on C. *repanda, lepida,* and *punctulata* show no such modification, or pattern modification of any other type so far as has been noted. Specimens stimulated by a temperature of 37°C. in the fall and forced through the winter were modified only in case of the specimens which emerged *early,* January 1. Specimens which emerged in the spring earlier than the normal were not modified. One specimen of *C. hirticollis* (Fig. 566, Pl. XXXI) coming through without any winter was very much smaller than the normal. A specimen of *C. lecontei* shown in color plate XXIX, figure 556, was different in form, the abdomen being broadest at a point not usual for *lecontei.*

One of the patterns of *tranquebarica* produced in this way (Fig. 459) was one of the most striking modifications obtained.

Thus so far as the species which show modification are concerned the modification appears to be in *definite directions* and the modifications of *C. tranquebarica, C. hirticollis,* and *C. limbalis* are in the general direction in which the modification of the pattern plan has proceeded in many patterns which have deviated from it in course of their evolution. The experimental results further show a basis for the interpretation of the geographic variation of the group which is our next topic for consideration.

GEOGRAPHIC VARIATION OF PATTERNS

C. tranquebarica, very widely distributed in North America, (Pl. XXII) shows great variation in color and markings, but the extreme forms are comparatively rare and confined to the Pacific states. Plate XXI shows the classes into which the patterns of this species may be divided and their distribution. The graphs represent the distribution of the per cent of classes shown by the figures below for specific localities. It will be noted that types *g* and *h* which correspond in middle band characters occur occasionally as extremes especially in Kansas and Texas localities, while west of the rockies where the summer and springs are dry and favor high soil temperatures these types are fairly common. This type of marking with middle band reduced at the margin makes up a considerable percentage of the individuals collected at Hagerman, Idaho; San Bernardino, California; Provo, Utah; and Las Vegas, Nevada; but they are nowhere the dominant type. In certain Nevada localities the retirement of the middle band appears to begin at the inner end and the withdrawal from the margin follows only in very reduced types. The type with the middle band withdrawn occurs in southern and western localities. Twelve per cent of the specimens from central Texas show middle bands like those modified in experiment. On the whole there is a correspondence between high soil temperature and the reduced type of markings which accords with the experimental results.

Plate XXIII shows the geographic variation of *C. scutellaris* and its varieties ranked as aberrations by Horn. The series of classes shown beginning at the extreme left are from the northern portion of its range in New England; passing to the right are shown very reduced markings at Raleigh, and very rarely any markings at all at Mobile and in Texas localities or points in western and west central states: Oklahoma, Kansas, Nebraska, and South Dakota, Colorado and New Mexico. In all localities, however, on and east of the Missouri River in the central states, there is a noticeable increasing in the size of markings as we pass to more northerly localities and to more easterly localities as far as Chicago. East of Chicago the marking of specimens from along the lake shores are not larger than those taken at the south end of Lake Michigan. As will be seen from the graphs (Pl. XXIII) the range of variation is least in the gulf states localities where the markings are most reduced.

There is further a noteworthy difference in the Mississippi Valley and Atlantic Coast forms. The humeral dot (*a1*, Fig. 48, Pl. V) is never present and the so-called posthumeral dot (*A2.3*, Fig. 48, Pl. V) is seldom so except in the more northern localities and is never large when present. It is never joined to the middle band (*A4*, *B4*). The markings are massed in the posterior half of the elytron on the costal margin. In the forms from Missouri River localities and eastward the humeral dot is usually present—always present in the more eastern form—and its absence is associated with extreme reduction of the markings in general. Thus patterns made up of a row of dots on the costal side of the elytron are the most numerous in Iowa localities and probably those just east of the Missouri River. Thus the selected classes of individuals are geographic in their relations and hence true classes. Further evidence for this statement is shown in plate XXXIV where the color differences are indicated, showing that the immaculate forms are further divided into races on the basis of color. Those of the humid southern states are green, and those of the western steppe, with its dry early summer following early spring rains, are red.

In full accord with the experimental results cited above are certain differences in patterns of two localities from which collections were made often. The larvae used in experiments were collected from a point just north of the village of Miller, Indiana, from a small area of oak dunes about an acre in extent. Adults were collected from this same locality during several years at various times in the season and differences in color and pattern were noted. Graph 10 is the distribution of classes in 200 individuals belonging to the generations of 1904 and 1905. This same graph is repeated above on a smaller scale with graph 11 added, which shows the distribution of classes in 51 specimens collected from the same area in April, 1906. Graph 12 shows the distribution of classes in a series of 60 specimens collected in the northwestern part of Gary, (600 ft.) (Pine Station, Indiana,) in April, 1906, showing the modal class to be *o* instead of *q* and a small percentage of individuals with markings joined. Graph 13 shows the distribution of classes in a series of 37 specimens collected in September, 1908, in which the same difference is shown. A difference in the distribution of classes is indicated by a comparison of Graphs 12 and 13. These differences are striking for one who is familiar with them. The differences between the Gary and the Miller locality were noted while collecting the species in the two localities during several years. The specimens collected in Gary showed those with markings joined as very rare. The entire series from the Gary locality show the same thing. There are also similar differences from generation to generation, in the catches from Miller. The difference in the conditions at Miller and in the Gary locality is striking particularly during the larval and pupal periods. The area in Gary is covered with scattered pines and in places from which some of the specimens were collected cottonwoods occur. The area is one of lake sand on which cottonwoods grow up and are succeeded by pines and the pines by oaks. The Miller locality is an oak dune area with well-established growth of oaks. One mile south of the Gary locality are oak covered ridges. Specimens from here are of the usual type taken in the Miller locality. Many of the pines had been cut off the pine belt in Gary where my specimens were collected. It is about as open as the cottonwood belt where evaporation from the porous cup atmometer is about twice that of the oak dunes in which the Miller specimens were collected. The soil temperature goes very high in the Gary locality.

Distance below surface	Temperature in degrees C Air 36 C
1 1-4 cm.	47
3-4 cm.	38
8-9 cm.	35
10-11 cm.	33
12-13 cm.	32
17-18 cm.	30

These forms pupate at a depth of 15 cm. and thus at a temperature of 31°C. on the warmest days. The temperatures in the shade in oak covered sand dunes are much lower being about 27°C. under the same conditions.

Plate XXV shows the division of the various subspecies of *C. purpurea* into classes. Here the primary division of the group, shown in the immaculate form in the center of the group which is very rare, is an habitudinal one—those at the left are the patterns of a series of races which inhabit level ground usually among scattered vegetation. To the right are those that occupy steep banks, particularly clay banks. Classes *a* and *b*, *cimarrona*, and *t*, *10 guttata*, do not appear to be so differentiated and accordingly the graph perhaps should have been reversed with the generalized patterns in the center, though further investigation would be necessary to determine this. The present arrangement is based on resemblances between the two, *cimarrona* and those at the left, and *C. 10 guttata* and those at the right. The distribution of the two groups shown at the right and the left of the center are shown in figures 471*a* and 472.

If one notes the localities represented by the graphs showing the distribution of classes, it is evident that there is no striking difference in the distribution of classes in Puget Sound, Massachusetts, and Colorado. The modal class for Manitoba, Topeka, and Chicago, is the same. This goes to indicate that the main line of separation is habitudinal rather than geographic.

Similar relation could be shown for other species. The main differences in patterns are primarily associated either with different localities usually separated geographically, or with differences in habitat preference.

The figures on plate XXVIII (Figs. 473 to 536) are arranged in parallel lines of similar patterns. Thus figures 473 to 485 are patterns of *C. tranquebarica* similar to those shown in figures 486 to 494, excepting 481 and 483 which are different species closely related to *C. tranquebarica*. In figures 486 to 490 are shown a series representing the typical patterns in *C. scutellaris;* it will be noted that these parallel those of *C. tranquebarica* with most reduced markings. Also figures 491 to 496 show the pattern of the Great Basin group of species and varieties to which *C. fulgida* is closely related. These parallel some of the patterns of *C. tranquebarica* and are in turn paralleled by those of other species. Concentric extension of the white likewise characterizes the patterns of the group. Figures 497 to 501 show a series of patterns in *C. pulchra* which are roughly parallel to those of *C. tranquebarica* and very closely parallel to those of *C. scutellaris*. The commonest pattern of this species is, however, figure 498; 499 and 501 being rare and collected only near Alpine, Texas.

Figures 503 to 505 show the series of patterns of *C. longilabris* which parallel the patterns of other species shown above and below.

Figures 506 to 518 show a remarkable and long series of patterns of *purpurea* parelleling the entire *tranquebarica* series without the addition of other species. The entire series is however different than the other series especially different from the *tranquebarica* series because of the short humeral lunule which always stops with spot *A2.3* while that of *C. tranquebarica* is made up of *A2* and *B3* in oblique combination (see Fig. 49, Pl. V). Figures 522 to 527 show the markings of the *C. sexguttata* group which parallel those of the other groups quite well throughout a series of five types. Figures 528 to 536 show a series of types belonging to five closely related species. The patterns at the extreme right show extension of the white which appears to have occurred as a tendency taken at any point in the series represented; thus figures 520 and 521 belong with 488 and to the same species. Figure 519 belongs with 531 and represents a different type of extension.

While a general parallelism is shown by the series of patterns, there is also a characteristic series of small differences belonging to the usual types of most species. This indicates that *specific* characters in the color patterns are matters of detail and any definitely directed *specific* or *racial* tendencies would have to be based on a consideration of such details rather than the general plan of the pattern and the general parallelism shown in the group of figures just discussed. While *specific* patterns are often very closely parallel, one who is very familiar with them can identify the species from a single elytral pattern in the vast majority of cases.

Considering the pattern of the rest of the group, represented in figures 473 to 537, *C. formosa* and its varieties is distributed on the

Atlantic coast and for some distance inland in Massachusetts to Maryland where the markings are of the type shown in figure 532 and slightly wider with the all joined at the side. The sharp forward bend of the middle band is characteristic of the eastern forms. *C. formosa* is distributed about the sand dunes of Lakes Michigan and Erie and through the sand areas of the central states, the distribution being very nearly like that of *C. scutellaris* except that *formosa* is wanting from Virginia to Texas along the Atlantic and Gulf Coasts.

The markings of the western Mississippi basin forms are broad as shown in figure 531, plate XXVIII, while in the more southern and western forms from Texas, Colorado, and Oklahoma are characterized by a middle band tending to be straight across the elytron.

The species which stands close to this is *C. venusta* (Figs. 533 and 534). The pattern is similar to that of *C. generosa.* It occurs only in sand areas of the great plains. The southern representatives have markings similar to figure 531 in width, but in Manitoba there is a tendency to the extension of the white as shown in figure 534. *C. limbata* is a closely related species which is taken only in blowouts in sand hills of the western Nebraska region and of Manitoba. Figures 535 and 536 show typical patterns. They do not vary greatly geographically.

C. ancosisconensis and *duodecemguttata* are invariable species (Figs. 528 and 529), *repanda* a subspecies of *12 guttata* distributed almost everywhere east of the Rocky mountains in the United States and Canada. Specimens from Louisana, Manitoba, and Virginia do not vary appreciably. The larvae inhabit very moist soil and soil temperature cannot be of any magnitude. The habitat and larval habits are such that variations due to differences in temperature and moisture are not common. If the soil becomes too dry the larvae leave it and dig a new burrow in soil of the wetness required by the species. Since they occur near water courses, this tends to keep larvae in similar conditions no matter in what latitude they occur. The variation of *oregona*, a related species, has not been studied.

C. hirticollis occurs on the sandy shores of the sea, lakes, and rivers from Vera Cruz to California, the Great Lakes, and Massachusetts. The pattern which is shown in figure 330, plate XVI, is quite invariable as compared with the rest of the species considered. High temperature experiments performed with these showed clearly recognizable modification in which the pattern duplicated Southern and Southwestern forms. The experiments and geographic and other variation are likewise parallel.

C. sexguttata has been studied and shows peculiar variations. Specimens from the Northeastern United States and the region of the Great Lakes have well developed markings (Figs. 525 and 526, Pl. XXVIII).

The same is true of Texas specimens. Specimens from E. Tennessee are reduced as in figure 523 and those from eastern Kansas are usually immaculate with a few like 523.

C. punctulata representing the Mexican group, has been studied and while widely distributed fails to show pattern varieties and did not show any modification when subjected to 40°C in the experiments. It also shows no geographic variation in markings. *C. lemniscata* shows the vitta broken in about seventeen out of seven hundred and fifty individuals. These patterns are like *luteolineata* (Fig. 24, Pl. III). *C. carthagena, haemorrhagica* and *C. gabbi* of San Diego, California, show a tendency for the markings to disappear by the spreading of pigment over the areas of the markings.

COLORS OF TIGER BEETLES

CAUSES OF COLORS

The pigment present in the cuticula of *Cicindela* is essentially all in the primary cuticula (Fig. 1). This pigment has been demonstrated by Gortner to be melanin and not the compounds stated by Tower (1906). This pigment is, in all the elytra observed, either brown or black. It is the result of the oxidation of tyrosin or related compound by tyrosinase (Riddle, 1909). In the case of all elytra examined in transmitted light which covers nearly two hundred species no color but dark brown ranging to black has been observed, no matter what brilliant spectrum colors were present in the elytra as view in reflected light.

Professor Michelson has made a study of the causes of the bright metallic and spectrum colors in various insects and feathers and has found that the colors are due to very thin surface films, metallic in character. He has very kindly examined elytra of several species, including *Cicindela chinensis* Dej., several varieties of *C. limbalis*, and several color varieties of *C. scutellaris*. The colors of the first two differ in different parts of the same elytron, the second named species showing blue and red and differing sometimes in the same population from black to green or blue, red, etc. The first two species gave results too indefinite to report. The third species, C. *scutellaris*, occurs on the Atlantic coast as a brilliant green form with some dead black forms among them in the same population; and in Kansas and Oklahoma the population is a flame red. The red *scutellaris* from Kansas showed a "preponderance of red in the spectrum, negative phase change at red end of spectrum, and positive phase change at blue end. The green, east-coast forms showed excess of blue-green with positive phase change at red end and negative phase change at blue end." The black form which occurs as a part of the general population with the green is without trace of color and acts like a piece of black paper. They are merely without the film over the surface.

Professor Michelson states further that the colors are chiefly if not entirely true surface or metallic colors. They are produced by a film of ultra microscopic thickness probably less than a ten-thousandth of a millimeter. He is inclined to attribute differences in the colors to differences in the chemical constitution of the film and color changes during ontogeny to changes in chemical constitution, but states that this would be very difficult to demonstrate on account of the minuteness of the film. The work of Heylaerts (1870) (see page 48) would seem to indicate that physical conditions or differences cause a change or difference in color in dried specimens.

Tower's figure copied by Folsom must be incorrect as he shows such a film as seen under the microscope. This line which he draws appears as a dark line under the oil immersion lens; it is probably a total reflection line which he misinterpreted under the influence of Professor Michelson's verbal statement, that surface films must be responsible for brilliant colors, which preceded the latter's investigation by several years.

The colors of the group which are on the whole exceptionally brilliant are to be attributed to a brown or black pigment either without or with any film or with films of varying effectiveness and with varying effects on the light reflected from the surface. A change in color with a change in the angle of incidence indicates the presence of metallic film.

ONTOGENY OF COLOR

One of the striking phenomena in connection with the study of the ontogeny of patterns is the ontogeny of color as opposed to pigment. Plates XXIX, XXX, and XXXI are devoted to this subject and show a series of radical changes in the character of the coloration associated with stages of development. Plate XXIX is devoted to the ontogeny of color in *C. scutellaris lecontei.* Figure 543 shows the beginning of color on the ventral side which consists of bluish reflections, at first about the center of segments which later become green. Later figure 541 shows purple reflections at points which remain so throughout without change, showing that changes do not always take place. The tip of the abdomen and trochanters appears not to have a surface film.

Considering the colors of the dorsal side and elytra we note that at the beginning the color is a yellow, the usual color of the cuticula when backed up by the tissues, with greenish reflections. After a little time green color begins to appear more prominent and the elytron of this normally brown species resembles the green form of the Atlantic coast (Fig. 553), differing only in lacking bluish reflection. From 3 to 15 days yellow reflections are at their maximum. Specimens occasionally are collected in this stage (September). After this the color begins to shift to red or dull brownish red, but has still greenish reflections in some individuals which gradually disappear with hibernation. The reddish reflections loóse luster and turn to a dull brown by the time the adult dies in the latter part of June after reproducing (Fig. 551). Important differences occur between individuals collected at different times of year.

Figures 559 to 562, plate XXX, show the development of the color in *C. hirticollis*. Here again the color begins as green and gradually shifts to brown or reddish brown. There are no green varieties of this species but it often shows greenish reflections in the adult condition. This is more pronounced in fresh individuals.

Figures 563 to 565 show the development of the color in *C. purpurea;* the first stage shown (Fig. 563) compares favorably with some forms of the variety *graminea*. As time goes on the color shifts to red over the upper surface of the elytron and the blue margin shifts to green, both shifts being down the spectrum. Black specimens occur with this species in the locality where the larval stages were collected for these observations.

C. purpurea limbalis shows a similar series of stages, and the shiftings which are similar to those in the form *purpurea-graminea-auduboni* shown above. In general during ontogeny in the species noted the color shifts down the spectrum as the cuticula hardens and pigment appears. In fact from blue to green the change is direct; but in passing from green to red the orange and yellow are not noticeable or at most occur as slight reflections; green changes to reddish green, red, and finally a dingy brown almost black in a few individuals collected in August and September with the new generation. A series of individuals killed, pinned, and dried so as to show a series from the beginning of color development to completion, is remarkable in that the earliest stage when dried is dull black, the second purple, the third blue, and individuals in the green stage (Fig. 573, Pl. XXXI) usually turn fiery red on drying (Fig. 576, Pl. XXXI). Heylaerts (1870) performed experiments on color changes in some European species. Brown specimens of *C. hybrida* when heated to 102°C. turn green and remain so for a short time when exposed to the atmosphere. The change to brown is hastened by blowing the breath on them. They remain green in a sulphuric acid desiccator. Green *C. campestris* turn blue when similarly treated. These changes accompany the almost complete removal of moisture from the surface film and are in the opposite direction as compared with the ontogeny changes and the changes which take place on drying of fresh immature specimens. The cause of these physical changes is unknown. Other shiftings in color have been noted; one of these in *C. lepida* is of particular interest as the change is in the direction opposite to that already noted. *C. lepida* has the elytron nearly all white but such parts as are pigmented are green in the adult. When the pigment begins to develop it is a brilliant gold and remains so for several days, finally changing to a dark green. In this case the change is the only one of the kind noted. Golden yellow blending with green is commonest in *cuprascens sperata, circumpicta,* and related species. These may shift from green to brown through yellow instead of red but their ontogeny has not been studied.

Even the dull species like *C. 12 guttata,* and *repanda,* and occasionally *C. punctulata* show more green in the early stages and turn brown as they mature. The early stages of *C. tranquebarica* are blackish green, gradually turning bronze brown as more pigment is developed. *C. formosa* is at first reddish and gradually changes to brown; some individuals collected in the autumn are red.

RELATION OF ONTOGENETIC STAGES TO GEOGRAPHIC RACES

First of all it should be noted that there appears to be no good reason for assuming that the biogentic law holds good with reference to these color changes; it would be only the most radical adherent who could see it applying. However in a general way the developmental stages of a given species, like *C. scutellaris lecontei,* may practically reproduce the color of another variety in ontogeny. Compare figure 546 with figure 553, plate XXIX. The stages in the development of typical *C. purpurea* do quite exactly duplicate some of the races recognized. Thus the stage shown in Figure 563 practically duplicates the color of *graminea* while Figure 564 duplicates some of the specimens of the subspecies *10 notatta.*

Again in Figure 572 appears an ontogeny stage which resembles very closely the variety *denverensis* but is less yellowish; *denverensis* also usually lacks the blue green margins, though the green is purer and brighter along the margin, showing a difference comparable to that seen in nearly all specimens of *purpurea.*

C. hirticollis shows a stage in the development of color (Figs. 559 to 562, Pl. XXX) which corresponds very closely to the race of the species occurring on the Pacific Coast. In addition to this it shows slight reflections of the bluish of the bluish drab forms of Vera Cruz. Reddish brown forms occur in southwestern Kansas.

Occasional specimens of *C. tranquebarica* collected in Massachusetts, show the dull green occurring in ontogeny. Similar greenish reflections occur in the western forms, but this blends with dark color instead of brown.

The light wine color of the high altitude form of *C. formosa* (Salida, Colorado, 7000 ft.) is duplicated in the ontogeny of color in *C. formosa* from near Chicago. Specimens which have this color are sometimes collected in the late summer near Chicago, but none have been taken in the spring.

C. punctulata appears not to possess a film such as described, as a rule, and the changes during ontogeny are not marked. The brilliant green forms which occur in the southwest have no counterpart in ontogeny.

Nearly all the species of the *tranquebarica* group, as well as many others, show a great series of colors. The following shown in Table II occur:

TABLE II
Showing Colors Occurring in Several North American Species

	Black	(Blend)	Brown	(Wine)	Red	(Blend)	Green	(Blend)	Blue	(Blend)	Violet	Orange	Yellow
scutellaris	x		x	x	x*	x	x	x	x		x	*	
purpurea	x		x	x	x	x	x	x	x				
sexguttata	x						x	x	x		x		
tranquebarica	x	x	x	x		x	x	x	x				
nigrocoerulea							x		x				
oregona			x	x**			x	x	x				
formosa			x	x	x								
hirticollis			x		>		x		x ***				
repanda			x		>		x						
willistoni			x		>		x						
fulgida			x	x	x								
pulchra				x									
anthracina	x						x	x	x				
pimeriana							x	x	x	x			
cuprascens			x	x			x	x				x	
lepida							x	<				x <	x

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*Reflections in western forms.

**Reddish brown.

***Dull bluish drab. Vera Cruz, Mexico.

In *scutellaris, purpurea, anthracina,* and *sexguttata* black and green forms are mixed, i.e., the species are dimorphic. The same is probably true of *tranquebarica,* as *plutonica* appears to be rare and occurs in California where the usual population is green. The physiological condition in which no metallic film is secreted is closely related to one in which a metallic film producing green is secreted.

The secretion of a film which lies at the outside of the primary cuticula is the first work of the hypodermal cells. It would seem that the secretion of such a layer might be inhibited by environic stimuli at a critical stage in the life of the pupa, but there appears to be no experimental results showing whether or not this is true. If environmental conditions do influence the occurrence of black and green, climatic conditions applicable to all species are not alike (see p. 52).

In the case of *C. scutellaris* the green and black forms have least pigment developed in the elytra (black is accompanied by a similar amount), and green in ontogeny is accompanied by least. The amount increases as the reddish color comes in, in *lecontei.* The amount of pigment in the brilliant red western form is intermediate between the green form and the dark red *lecontei. C. splendida,* very brilliant, shows much less pigment than *limbalis,* which is dull.

Many species, particularly *purpurea* and *pulchra,* show more brilliant colors along the elytra margin where white markings usually occur. This is noticeably true in *purpurea,* which in the subspecies *cimarrona* has a complete white margin in many specimens. As a rule when the areas commonly occupied by markings become pigmented the colors in these areas are more brilliant. W. Horn (1915) has called attention to this. As has been noted, the elytral surface of most tiger beetles is made up of small hexagonal pits which probably correspond to the hypodermal cells which secreted it (Fig. 1, Pl. I). The ridges between these lie over the boundaries of the cells. In the elytra of *C. purpurea* these pits are smaller in the blue-green margin. The same is true of many other species as shown in Table III.

While many colors such as green and greenish blue, red, etc., in early ontogeny change to colors of longer wave length during ontogeny and later life, such is not true during ontogeny at least in the case of such purple specimens of *C scutellaris.* These are rare and only a few specimens from Starved Rock (Utica), Illinois, have been found; some of these are purplish brown, but one individual was secured in the larval stage and reared (Fig. 558, Pl. XXIX). It was purple from the beginning and never showed any tendency to change, though it was kept for a long time. The same is probably true of the purple forms of *C. sexguttata* which occur in eastern Kansas; purple forms of *nigrocoerulea* show no blends with the green.

TABLE III

The following table shows the relative size of hexagonal cups in various forms and parts of the same elytron, etc.

Species	Variety	Locality	Organ	Part	Color	Diameter in mm.
C. purpurea		Massachusetts	elytron	margin	green	0.0115
" "		Chicago	"	disc	red	0.0150
" "		"	"	margin	green	0.0115
" "	*denverensis*	Denver	"	disc	"	0.015
" *scutellaris*	*lecontei*	Chicago	"	"	brown	0.0150
					red	0.0150
" "	*scutellaris*		"	"	"	0.013
					green	0.0115
" "	*rugifrons*		"	"	green	0.0100
" "	*modesta*		"	"	black	0.0100
" *generosa*		Colorado	"	"	red	0.0150
						0.015 to
					blue	0.0225
" *chinensis*		China	"	disc		0.018 av.
					metallic	0.013

GEOGRAPHIC VARIATION IN COLOR

The black forms of *C. scutellaris* are found to occur in some New York localities, and some New England localities, but are less numerous than green ones. A complete catch from Providence, Rhode Island, for one season, including hibernated and freshly emerged forms, showed less than 20 per cent black individuals; a similar catch from Framingham, Massachusetts, gave no black individuals; 112 specimens from Aqueduct, New York, showed about 15 per cent black. Some localities in New Jersey show, according to Leng, a majority of black forms in spring. A small catch from Baltimore, Maryland, showed more than half black forms. At Raleigh, North Carolina, black forms do not occur, and I find no records for Virginia, North Carolina, and South Carolina; but black forms occur in Alabama, Georgia, and Florida. At Mobile a few black ones are found in the autumn but very few or none at all in the spring, according to Messrs. Loding and Van Aller who have been interested in them for several years. None are recorded for points farther west.

Black forms of *C. sexguttata* likewise occur in the eastern states, New Jersey and Pennsylvania, but not in the southern localities. Black forms of *C. purpurea* (see map, Fig. 472) occur in Illinois, Iowa

Minnesota, Kansas, Nebraska, South Dakota, Colorado, Utah, Wyoming, and New Mexico, but are very rare in eastern localities. Mr. C. A. Frost secured one bluish black individual in Massachusetts. The black forms of *C. tranquebarica* are recorded from a single locality in California. No black forms occur in the localities where black forms of other species occur though blackish green forms occur in the Pacific States and blackish brown, in the Gulf States. Likewise there is no correlation between geographic conditions and green forms. *Scutellaris* is green on the Atlantic coast, *purpurea* in the central and northern great plains, *tranquebarica* on the coasts and coastal mountains.

Exclusive of black forms which have just been discussed the geographic variation of colors in the species belonging to the *tranquebarica* group, may be stated as follows: Geographic variations in color are of special interest in the case of *C. scutellaris;* I note green forms predominating in all specimens in the Atlantic Coast and Gulf States. Bluish reflections characterize these as a rule, particularly in some localities where occasional blue forms occur (Fig. 470 *a*).

In Texas along the northeastern border near Oklahoma forms occur with a decided golden cast which in series in some localities range from bluish green through green with golden cast to flame red like figure 554, plate XXIX; north of this flame red predominates. Forms with flame red elytra and green or blue thorax occur west to the Rio Grande, occupying a triangular area with its apex just north of the Black Hills and eastern point near Topeka, Kansas. Points a short distance west of the Missouri River such as Topeka, Kansas, and Superior, Nebraska, show great variation in marking and all intermediate color conditions between the forms with flame red elytra and those of the dull brown and wine color occurring to the east and north of the Missouri River. The most brilliant wine colors occur between the Mississippi and Missouri Rivers and in Manitoba; near Chicago the brilliant wine colors are not usual, but greenish browns and greenish individuals are common. There appears to be no close correlation between the distribution of these colors and any mapped distribution of factors.

C. purpurea is very variable; figures 471 *a*, 472 show color varieties of this species. In general among the groups in which the markings are withdrawn from the margin, the forms with the upper part of the elytron reddish and its margins green are most widely distributed, extending almost throughout the range of the species except the Pacific coast specimens which are golden green (Puget Sound, 10 ft.). The eastern forms are of the typical red elytroned type. In the entire Mississippi Basin, Great Plains, and Salt Lake Valley this is mixed with green and black forms, the latter two predominating in the western Great Plains. In the New Mexico localities dark brown forms (*cimarrona*) occur. There is no correlation between color and mapped climatic conditions unless it be rainfall.

Considering the *purpureas* in which the reduction of markings leaves only a small dash at the margin of the elytron, one notes that the wine colored specimens are distributed throughout the region of the Great Lakes and in Manitoba and generally westward to the Missouri River, and Colorado. This type is distributed in a general way north of about 41 degrees North Latitude and has the thorax the same color as the elytron. The forms *splendida* and *transversa* are similar in color but have the thorax green or blue and the elytron either red or wine color, they are distributed south of the form with red thorax and in the eastern part of the range are less brilliant than farther west. The more western forms have brilliant red elytra similar in color to that of the red *scutellaris*. Mixed with these are the green forms; in western Kansas and Colorado, especially, they occur with the red forms and are often taken in coitus with them. The green form is evidently merely a color aberration of the red form.

The color variation of *C. tranquebarica* is not striking over the entire area east of the Rockies. Nearly all are simply dull brown. Specimens from the moist southern states are usually duller blackish brown than the northern forms. No striking color varieties occur even east of the Pacific states and Idaho. In some parts of eastern California (Bridgeport) they are brown, while only a little way west they are green; further surprising differences were found in Nevada. At Caliente the writer took brown *tranquebarica* and blue *oregona*, while at Las Vegas he took green and bluish *tranquebarica* and no *oregona*, which occur there and are probably green also, but there is no apparent reason why *oregona* should be blue or green and *tranquebarica* brown in a region where both are likely to be green.

C. generosa is brown and wine color in eastern localities and where *purpurea* is similarly colored. Near Chicago the colors are similar. At Topeka, Kansas, the color varies considerably, reddish, bluish, and greenish brown occur. South, and southwest from this point the specimens are progressively redder. The most brilliant forms are the red ones from western Oklahoma, western Texas, and Colorado. At low altitudes these are golden red. Wine red occurs at high altitude (Salida, Colorado, 7,000 ft.). *C. hirticollis* has already been discussed (see page 49). With the exception noted there is little variation and distribution is transcontinental and from the Great Lakes to Vera Cruz.

EXPERIMENTAL MODIFICATION OF COLOR

This is frought by many difficulties on account of the remarkable series of colors and color changes occurring in ontogeny, and the usual early death of individuals reared under experimental conditions. Figure 555, plate XXIX, shows an experimentally modified individual of *C. lecontei.* The presence of the yellowish color in the markings indicates that secondary cuticula has been secreted with the air spaces between, in quantity sufficient to give the opaque appearance to the markings. This specimen in particular was known to have died 15 days after it was dug out of the soil, which is not until the cuticula is well hardened. Its markings are reduced below anything ever found near Chicago. The color shows an unusual amount of yellow and approaches most nearly to some of the western forms of *scutellaris* (Fig. 554) though not exactly like any forms known to occur. This particular individual showed more yellow and was most generally modified, leaving no doubt as to the fact that color modification had occurred. Three other individuals, all of which lived long enough to show the development of opaqueness in the white markings, were produced and showed green of unusual clearness from reddish brown and suggestive of green forms rather than the parent stock of *lecontei.* All these were in dry conditions. The warm moist experiments showed green forms but not clearly differentiated from ontogeny stages in part due to early death.

Three specimens (Fig. 557) were brought through successfully in icing experiments and lived two weeks or more. Two of these were characterized by broad markings and dull brown elytra and rather striking differences between the color of the head and the thorax, the latter being quite green. Figure 557 shows considerable modification of form and size not noted in the other two. The very rounded ends of the elytra, and square shouldered character was quite striking and in direct opposition to the usual tendency shown in the rest of the group.

Figure 556 shows a specimen brought through at 37°C. with marked acceleration of development. This individual was small, slender in the head and thoracic region, with the elytron widest in the region behind the middle band. The color is much brighter and freer from dull brown reflections than that of the normal specimens, having a decided brilliancy to the color. This specimen was kept alive until the opaque appearance of the markings was well developed. This body form is characteristic of many specimens from the extreme southern states. There is a noticeable general tendency toward this general body form in all individuals reared in high temperature.

Experiments were performed on *C. hirticollis* which paralleled those noted on *C. scutellaris*, but with results on markings and none so far as color is concerned. It is probable that the experimental individuals showed more green than others, but the difference is too slight to justify an unqualified statement to that effect. One striking result was obtained in the experiments where the temperature of about 37°C. was maintained on larvae which had not hibernated; one small individual was obtained (Fig. 566) which however retained all the striking characteristics of the species.

Experiments on *C. tranquebarica* were successful. Specimens reared in temperature of 37°C. and much moisture (Fig. 570) showed the dull blackish brown which characterizes the colors of some of the specimens from the moist southern states. This color was not uniform throughout the series so raised, but was much commoner than in the case of specimens reared in hot dry conditions, as these are more brilliant (Fig. 569). A number of specimens were iced but only one of these was especially peculiar (Fig. 568). This was decidedly *more red* than any others seen in the course of my studies. Some of the iced specimens were unusually dull, however, and no uniform results were noted except that the heads were uniformly greener.

C. limbalis was subjected to high temperature. In the moist conditions dull colors were obtained. Figure 577 shows one of the high temperature individuals in which the color is deeper red and the reflections more striking blue than in the normal specimen at this stage (Fig. 575). 579 which shows an individual subject to high temperature in moist conditions is more generally dull green. 578 shows an iced specimen which is similar to the warm moist individual. These differences are slight and not very convincing, but the individuals are different from any reared or collected under other conditions.

Experiments of a similar character were performed on *C. punctulata* but appeared to be without results. A similar series on *C. lepida* were likewise without results.

RELATION OF COLORS AND COLOR PATTERNS TO CLIMATE

After a thorough study of the subject and comparison of the distribution maps of several species with maps showing the rate of evaporation of water for the year, the evaporation of water from the porous cup atmometer from April to September, the ratio of rainfall to evaporation, mean annual temperature, temperature April to September, and with maps showing cloudiness, humidity, rainfall, etc., it was demonstrated that the distribution of color varieties, and pattern varieties even where the types are quite distinct, is not correlated with the conditions shown on such maps.

In general such correlation is closest in relation to rainfall, but this correlation is not so good as one would expect (Fig. 470 *a*, Pl. XXIV). This is perhaps to be expected in the case of species which belong to local conditions which is true of most of the species of Cicindela. This subject has been discussed in some detail (Shelford, 1911). Here it was shown that species which were distributed in a major climatic habitat had a distribution correlated with the distribution of vegetation, which in turn is correlated with the distribution of climatic conditions. I showed further that species such as *C. tranquebarica* traversed almost the entire continent without much variation by virtue of living in moist soil, due either to climatic moisture or to local stream moisture or lake-shore moisture. *C. scutellaris, C. purpurea* and most of the other species noted are found in some special kind of soil such as sand containing a little humus (Shelford, 1911, 1913b) or steep clay banks or some other restricted situation. Taking *C. scutellaris* for example, this species being found in well drained or dry sand containing a little humus and bound by scattered vegetation throughout its range, it is to be expected that the distribution of the species will be correlated with some sort of measured soil conditions such as soil temperature, soil wilting coefficient, or the like; but no such conditions have been recorded or mapped. There is some evidence of soil effects in this species (see Fig. 558, Pl. XXIX). Some specimens from the very coarse sands resulting from the weathering of St. Peter's sand stone, near Utica (Starved Rock), Illinois, are purple. No purple forms have been taken elsewhere. Two specimens from sandy clay (Suman, Indiana) had an unusual silky appearance. When soil temperature work under way is published, I shall attempt to make use of the extensive records which have been accumulated for the purpose of working out correlation between conditions and color and pattern varieties. Conditions associated with altitude influence color in some cases, but there is no unity of conditions or colors.

GEOGRAPHIC CENTER OF THE GROUP ON THE BASIS OF PATTERNS

The usual criteria for the center of distribution (Adams, 1902) indicate that the Oriental region or at most the Oriental and Ethiopian regions (shores of the Indian Ocean) are the geographic center or center of distribution of the group. The first evidence presented which indicates this is found in table I, in which eleven groups of species are shown to occur in the Oriental region and in other regions, while not more than six occur in any one other region and at the same time in still others.

Patterns are divisible into three great groups: first those without the spots at the base and along the inner border of the elytron shown to the left of the bottom of figure 580; these patterns represent the usual type of the group and are world wide in distribution. The patterns to the right of these are those with the basal spot and the two spots along the inner border, shown on the map by the stippled area; this includes a number of pilosity groups and thus represents considerable diversity. The group in which the middle cross band (*4*) is oblique in the reverse direction as compared with that which is usual in the group as a whole, is shown by small circles. This is essentially confined to the Oriental region. There are a few species in Africa which show this and which appear somewhat related on the basis of pilosity, but circles are omitted. The group of species and patterns shown at the extreme right and represented on the map by the short oblique lines constitute a group divided between the Oriental and Australian regions.

An over-lapping of the various types in the Oriental region is evident. This would place the center for the group in that region but several African species appear to be most primitive from the standpoint of kind of patterns shown. It accordingly seems best to consider that the lands adjoining the Indian Ocean constitute the center of distribution of the group.

GENERAL DISCUSSION

The evidence which must support any conclusions drawn is of such a character and drawn from so many sources that the presentation of a few lines of evidence and the conclusions forthcoming from them can best follow the general presentation of data and minor conclusions on the preceding pages. Since color and color pattern are quite distinct so far as laws governing them are concerned, the discussion of the two will be separated.

PATTERN TENDENCIES

Under this head we are concerned with (a) the original type, (b) the most characteristic elements and combination of original characters, (c) general laws of pattern modification applicable to groups of species, (d) laws applicable to particular species, and (e) laws applicable to subdivisions of species.

As has been noted the number of directions in which modification has preceded are numerous and any statement of such directions is difficult and has led other authors to make general statements regarding the modification of patterns which were general enough to apply to a large number of species.

The earliest account of variation in the color, or markings or the patterns of tiger beetles is that of Dr. Geo. H. Horn (1892). He took the markings of *C. tranquebarica* Herbst as the underlying type "from which all forms observed in our Cicindelas have been derived". He bases this statement on the fact that it is the so-called humeral lunule, middle band, and apical lunule which give similarity to the patterns of the genus. He states that modification occurs in any one of four ways:

A. By progressive spreading of the white.
B. By gradual thinning or absorption of the white.
C. By fragmentation of the markings.
D. By linear supplementary extension of the white.

These tendencies are all recognizable, all of them occurring in the course of individual and geographic variation of single variable species.

Walther Horn (1908) in Genera Insectorum discussed the patterns from a somewhat different point of view. He states that in the ideal sense the markings which he recognizes as the humeral, apical, and middle spots are made up of 3 humeral, 4 middle and 3 apical spots as shown in figure 290, plate XV, and 333, plate XVI. Thus he calls the markings which are most characteristic of the group the *Marginal Component*. He calls the median basal spot of the elytron the *Basal Component (B1)* and the marking along the suture or anal border of the elytron the *Sutural Component*. He recognizes also such patterns as those shown in figures 241, 243, 248, as *Dispersion Component*. He states that this analysis is for taxonomic purposes only and not based on ontogeny. He recognizes the most important tendencies toward joining of spots, in addition to the general plan outlined in G. Horn's four statements.

The work of these men is here cited to show the fact that various generalizations have already been made showing that the patterns conform to a general plan of spots or bands which have been similarly interpreted, though not exactly the same, by two authors with wide experience in the group.

For the purposes of illustrating what may be determined in the group in the way of general tendencies (p. 36) and the patterns of *interrupta*, *interrupta* subsp. *gabonica*, *flexuosa* (Pl. XII), *tranquebarica*, and *purpurea*. And for a second illustration take the same species substituting *scutellaris* for *purpurea*.

First noting *interrupta* and *gabonica*, (Figs. 156, 156 *a* and 165, and 165 *a*) one finds that the cross bands clearly recognized in Coleoptera, especially *Chrysomelidae*, and *Lepidoptera*, and which appear in the tiger beetle group especially in the patterns associated with *interrupta* (Pl. XII), and which appear in all the species in which ontogeny was studied, are present. In *gabonica* it appears that through individual variation the characteristic joining to make the "middle band" is indicated. This occurrence of cross bands as noted and the variations of *interrupta* together with the light stripe in the region of joining of the cross band *4* with cross band *5.6* which occurs in the ontogeny of the patterns of *scutellaris* constitute the evidence for the line of development suggested.

The *second tendency* to be noted is the shifting of the spots near the sutural or anal border of the elytron out of line with the cross band with which are properly associated. This is shown in figures 156 and 156 *a*, plate XII, *interrupta* and in figures 153 and 154 in *flexuosa*.

The *third tendency* to be noted is the loss of the three small basosutural spots (*B1, C2.3, D4*, Fig. 49, Pl. V). This usually takes place in a definite order if individual variation may be trusted as an indicator. At least these may have disappeared in some definite order leaving the typical pattern of *tranquebarica* as shown in the controls of the experiments (Figs 456*a′, b′* and 457 *a′, b′*). This type is shown in figures 31, 32, and 33, plate III, and the elements from which it is made are shown with others in figure 49, plate V. As further evidence of the longer persistence of *C3.4* see figure 125, plate X, and figure 145, plate XI, which are late stages showing the persistence of this spot after the more anterior one has disappeared.

The *fourth tendency* which may be noted is the tendency for the typical *C. tranquebarica* pattern to shift as indicated in the patterns which result from experimental stimulation during ontogeny. This is shown in figures 456 *a, b*, 457 *a, b*, 458, 459, and 460 *a, b*, plate XXVIII. These modifications have already been noted on page 39 but may be recalled briefly as follows: the forward and backward extensions of the inner end of the humeral lunule (spot *B2* drops out) disappear; the slight forward extension of the inner end of the middle band in the longitudinal stripe *C*(*C5*) drops out or loses identity. The withdrawal of the middle band from the elytral margin and reduction to conform with that of *C. purpurea (purpurea)* (Fig. 537, Pl. XXVIII) is the striking and probably the most important change best illustrated in 460 *a, b*,. Similar modifications in all high temperature experiments with *C. hirticollis* (some with C. *limbalis*) serve to clinch the argument for response in definite directions.

A *fifth tendency* is illustrated by *C. purpurea* as shown in the figures to the left in figure 537, plate XXVIII. The differences between the *purpurea* series and the *tranquebarica* series lies in the short humeral lunule of the former, which indicates a different tendency which perhaps constituted the original distinction between the patterns of the two series.

Turning to the *scutellaris* series one notes that markings are reduced by high temperature (Figs. 463 *a*, *b*,-, 464 *a*, *b*, -, Pl. XX). The original markings evidently included a middle band like *purpurea* (Fig. 512, Pl. XXVIII). As evidence for this note figure 490, plate XXVIII, which shows a reduced band present, and figure 115, plate IX, which shows one in ontogeny which does not persist in the adult at all in individuals from the central states. Stimulation of *scutellaris* during ontogeny by high temperature merely reduces the markings concentricly, withdrawing the middle band from the margin as well as from the centre. This is the type of modification which has led to immaculate forms in the south and southwest.

Cold extended the same markings, but the results are not so striking in general plan though perhaps equally general in application, as markings are lost in the same general order in many species if individual and geographic variation may be used as an indicator. First we have noted that *purpurea* is divided into two groups, one the steep-bank-inhabiting group and the other the level-ground-inhabitant. The latter (Pl. XXV, left, and Pl. XXVIII, Fig. 537) loses its markings in the manner suggested above, as indicated by the experimental results with *C. tranquebarica*. The outer end of the band being lost first. The other loses its markings as does *C. scutellaris*. Compare 486 to 490 with 506 to 510 and 522 to 525, plate XXVIII, which indicate the loss of markings of several species along similar lines, i.e., through retreat to the margin and then reduction of the marginal markings. Thus the response to high temperature represents a tendency present in many species.

The large confluent markings of Manitoba specimens and of those which have been subjected to cold suggest that a second type of response may be in the form of a concentric extension of the unpigmented areas. It seems evident that the mechanism in *C. scutellaris* may be thrown in either direction from the general average of the species.

I have followed through a series of marking modifications and shown evidence for the tendencies indicated. It would be futile to present further discussions of a similar type regarding other species, as particular weight is given to experimental results and such results are wanting in other species. The reader by an inspection of the figures which are particularly numerous and selected for the purpose will note that in many groups one species begins in pattern modification where another leaves off. This fact was noted by G. Horn (1892). In many cases an exact knowledge of the geographic variation of the species is not available, but figures 435 to 437, plate XVIII, show a series which is supported geographically. *C. curvata* which occurs in Mexico is first in the series, *dorsalis saulcyi* which occurs in Texas next, and *dorsalis* which occurs in New York and New England shows spreading of the white. This series is representative of one in which the patterns are of a specialized type, in which the media trachea is reduced. Forward curves in the humeral lunule are very rare; one specimen of *saulcyi* in the collection of Mr. Gestro in Genoa has this marking curved forward. The backward curvature occurs also in *trifasciata peruviana* but is rare. Figure 434, plate XVIII is probably this species.

Much detailed study and collecting is necessary to show that the differences which enable one to arrange a group of patterns in series really represent a series geographically or habitudinally separated, and the writer refrains from further discussion of such cases though others might be cited with little doubt as to their validity. The patterns in the illustration pages are arranged to show probable lines of modification. The large series of parallel trends shown in different groups leaves little doubt that the tendencies shown are highly probable.

Another tendency quite common in the Cicindelas is the degeneration of the media trachea. The shifting of the pattern in that region is one of the first modifications to take place if we may judge from the existing patterns and from individual variation. The complete breaking up of the system of markings appears first in this part of the elytron. This degeneration of the old system of markings has proceeded far in some species such as figure 16, *nivea* and figure 21, *tenuipes*. Here an almost entirely new system has grown up, but derived from the older one. These cases constitute our best evidence that these patterns are highly specialized. The morphological structures with which the pattern is associated, are modified; some of the important parts have degenerated.

In considering these patterns and the modifications which take place the reader must not fail to note that there are physiological problems to be considered and physiological work to be done. The explanation for the occurrence of pigment in some parts of the body and not in others may be very simple. In course of experiments concerned with the production of abnormalities, it was found that the labrum which is not pigmented in the species used, develops pigment in the area of wounds. Specimens with abnormal elytra which appear to be due to injury or irritation nearly always have reduced patterns, but no cases in which the white markings are extended are recorded. Thus it appears that the present adult areas of pigmentation and areas of ontogenetic and earlier pigmentation may be merely areas occupied by cells with a higher rate of metabolism. This in the normal elytron may be due to advantageous nutrition conditions arising from the morphology of the wing, or to special characteristics of the cells themselves.

BEARING OF THE COLOR PATTERN MECHANISM ON ORTHOGENESIS

Orthogenesis is commonly understood as evolution in certain direction as opposed to evolution due to the survival of certain kinds of variations out of a large fortuitous series. The chief points in the original contention of Eimer, namely, that progress in species formation has been along definite lines, has been so generally admitted that the remaining matters are concerned with such questions as: How definite have the directions of modification been? What are the causes of certain directions of modification being developed to the exclusion of others? Are the causes external or internal? Whitman has emphasized the internal causes, which is the tendency of all who come at the problem from the point of view of embryology, cytology, and modern genetics. The mystical nature of the question of the origin of a complex organism from a single cell, transmitted through the egg and the sperm of the entire series of details which are inherited, have fascinated men and led to the general acceptance of theories which involve the insulation of the bearers of herditary characters from the environment. The evidence at hand does not justify any detailed discussion of this problem but I will turn to the few things which appear to apply to the tiger beetle group.

The effects of high temperature on *tranquebarica* produce variations in the direction of shortening the longitudinal portion of the middle band and throwing this marking into an oblique position. This is also one of the general tendencies in a large group of tiger beetles. In *tranquebarica* it occurs as a response to stimulation, and in its races of unknown stability in regions in which high soil temperatures may be expected. It occurs in nearly half the species of the group of tiger beetles as a regular, probably hereditary character. The condition of the middle band seems to be due to a mechanism of response or modification, which is the same in these responses to stimuli and in the regular heredity trends. The problems of herdity then appear to be the same as the problems of development and modification of this elytral character of Cicindela. Perhaps the weakest point in the entire method of study and reasoning of those interested in problems of heredity is the apparent practical assumption that laws of heredity are not the same as laws governing characters, in particular organs, and as laws of response. The evidence presented tends to show that these laws are one and the same and are dependent upon a mechanism present in the elytra of many species of Cicindela. If this is what is meant by orthogensis this group illustrates the orthogenetic principle.

The illustration above is concerned, however, with only one of several kinds of tendencies which appear in the group. Still another principle is suggested by the experiments. If extension of the unpigmented areas is indicated by the experiments with cold conditions during ontogeny, which would be supported by geographic variation in many species, one is forced to the conclusion that different kinds of stimuli acting on the pattern mechanism produce different responses. One type of response is the extension of the unpigmented areas. From an inspection of the figures it appears that this may take place on the basis of a pattern in any stage of reduction. As a rule it occurs in correlation with some marked change in the basal structures of the elytron at least when the extensions violate the original plan of the pattern. The mechanisms of pattern heredity and pattern development possess the capacity both to respond to stimuli by changes in form and by the extension of the unpigmented areas. This extension of the unpigmented areas may take place in almost any form of pattern shown in the entire series and may be concentric or in part linear. This is shown in plates XII to XVIII and XXXVIII. The concentric extension at least would seem to constitute a sort of reverse principle to that illustrated by the changes in form resulting from my experimental conditions, such as high temperature. In dealing with definite directions of response which may be termed orthogenetic if desired, one must recognize progressive modification on the basis of a mechanism which may move in any one of two or three or more directions under the stress of external stimuli. Some evidence for a progressive series of modifications in the same direction running through a series of species in the tiger beetles is afforded by the experimental results. In general the pattern of *C. hirticollis* is more angular and as a whole conforms to the original ground plan better than that of *C tranquebarica*. The modification of the patterns (middle band) of *C. hirticollis* is in a direction toward that of *C. tranquebarica*, but is not carried so far as are the modified patterns of *C. tranquebarica*. *C. limbalis* is usually, in the *less* modified forms of middle band, about as far from the original angular type as are the *more* modified forms of *C. tranquebarica*. Stimulation of the mechanism of the middle band in *limbalis* at this stage usually throws the band still further toward that of *splendida* or typical *purpurea* (Fig. 537, Pl. XXVIII). Since the middle bands of the three species differ normally only in the extent to which such oblique shifting occurs, and each differs from the original plan to a greater degree than the other, the peculiar character of the direction taken must result from a similarity of mechanism in the different species concerned. Abundant evidence for stages in such shifting as fixed hereditary characters is found in many patterns illustrated in the plates, particularly plate XXXVIII. The series of three species thus show the same tendency, with respect to the middle band. This must be due to the existence of the same mechanism for heredity and response. The next step to important discovery probably lies in the direction of further analysis of the mechanism by experimental means, which may include surgical and mechanical experiments on the developing wing covers, and analysis by such methods are commonly used by the breeder.

BEARING OF THE PATTERN MECHANISM ON THE BIOGENETIC LAW

The data accumulated in connection with this study shows certain principles concerned with the application of the biogentic law. First the general plan of the pattern seems to be common to all insects. The ancestry of the insect group is too obscure to justify the assumption that any original ancestor possessed a wing with nineteen spots such as are shown in the elytron of Cicindela, or that such an ancestor possessed longitudinal stripes or cross bands. The evidence seems to indicate that the tiger beetle group shows a type of pattern mechanism described at length in the preceding pages; that this pattern mechanism is plastic at least in the more generalized species; that from this plastic mechanism certain definite lines of modification have been somewhat fixed and limited. So long as the ontogentic features are concerned with the general mechanism one is not justified in calling the appearance of certain spots recapitulations. They may fully as well be areas which are less favorably nourished or which are made up of cells with lower rates of metabolism (see p. 31). Either of these physiological conditions may be due to mechanical necessities in development in all insects primitive and specialized, and if so, why call them recapitulations?

Such evidences of recapitulation as do occur are found in the recurrence of markings in development which represent those occurring in related species or varieties. Thus, as I have noted, a curved middle band occurs in the ontogeny of some specimens of *C. lecontei* and duplicates a late stage in the loss of this marking as shown in figure 115, plate IX. Here a curved and degenerate form of this marking occurs temporarily during ontogeny and may perhaps be regarded as recapitulation. The application of the biogentic law must generally be followed with great caution in dealing with insect patterns and no doubt with many other phenomena.

SUMMARY OF CONCLUSIONS

PATTERNS

1. The color patterns of the tiger beetles are related to elytral structures but not casually; longitudinal stripes in which pigment usually occurs lie in the area of the chief tracheal trunks; there are seven cross bands in which pigment does not develop, the second and third and fifth and sixth of these are often joined to make one of each pair.

2. Pigment usually occurs about the bases of hairs which usually lie in the lines of the tracheae.

3. In ontogeny the elytra show a spotted condition corresponding to the system of cross bands and longitudinal stripes. The longitudinal stripes are usually more pronounced.

4. The characteristic markings of the group are composed of spots or elements joined in the longitudinal light stripe areas and areas of cross bands with the loss of various spots or elements which occur in ontogeny; joinings are sometimes oblique and when so markings are sometimes parallel with curved end of the elytron.

5. Certain particular types of markings made up of a few elements joined in a particular way characterize the majority of species of the group.

6. These markings as derived from the cross and longitudinal bands are angular; reduction of angles, straightening and turning into oblique positions parallel with the end of the elytron characterize modifications of markings. The response to stimuli (high temperature) is in the same direction.

7. Response to other stimuli appears to be in the direction of concentric extension of the markings.

8. The color patterns and structure to which they are related constitute a mechanism, the directions of movement of which are limited, i.e., easier in some directions than others; the color pattern plans break when the related structures do; hereditary changes and fluctuations due to stimulation during ontogeny are in the same direction; laws governing the mechanism are the same throughout.

9. These laws when applied to hereditary changes are apparently what is sometimes termed *orthogensis.*

10. It is not correct to assume that all manifestations of the wing mechanism which appear during ontogeny follow the biogenetic law.

COLOR

1. The brilliant colors of the group are due to thin surface films of material having properties of metals.

2. Changes in color during ontogeny are from green and blue toward red or brown, except in *C. lepida* in which it is from yellow (gold) to green; purples appear to stand apart from greenish blues and do not change during ontogeny or if so only slightly.

3. During ontogeny some species pass through stages corresponding to geographic races, but the biogentic law is of doubtful application, though green stages in ontogeny possess the same amount of pigment as green races and the reds and brown which come later are associated with more pigment but not causally.

GEOGRAPHY

1. The center of distribution of the group is about the Indian Ocean.

2. Geographic races and geographic distribution is not correlated with any observed climatic or meteorological conditions unless it be rainfall and in this case the correlation is not complete. This lack of correlation is believed to be due to a lack of records of soil conditions.

are

3. Experimental modifications nearly duplicate certain geographic races of the species concerned; these races occur in localities where conditions are probably similar to the experimental condition.

4. In the species studied in detail the more brilliant colors are in warm arid localities, reduced marking in warm localities, and extended marking in cooler localities.

BIBLIOGRAPHY

ADAMS, C. C.

1902. Southeastern United States as a Center of Geographic Distribution of Flora and Fauna. Biol. Bull., 3:115-131.

BATES, H. W.

1884. Coleoptera, Cicindelidae. Biologia Centrali-Americana, Insecta, 1, pt. 1, 1-18.

BRAUN, ANNETTE F.

1914. Evolution of the Color Pattern in the Microlepidopterous Genus Lithocolletis. Jour. Acad. Nat. Sci. Phila., (2)16:105-168.

BACHMETJEW, P.

1902. Experimentelle Entomologisches Studien. 1:Leipzig.

1907. Ibid. 2:Sophia.

COMSTOCK, J. H., and NEEDHAM, J. G.

1898. The Wings of Insects. Amer. Nat., 32:43, 81, 231, 335, 413, 561, 769, and 903.

CHILD, C. M.

1915. Senescence and Rejuvenescence. Chicago.

CRIDDLE, N.

1907. Habits of Some Manitoba Tiger Beetles. Can. Ent., 39:105-114.

1910. Ibid., 42:9-16.

HEYLAERTS, F. J. M., JR.

1870. (On *Cicindela campestris*). Tijdschrift voor Entomologie, 13:178-179.

EIMER, G. H. T.

1898. On Orthogenesis and the Importance of Natural Selection in Species Formation. Religion of Science Library, Chicago.

ENTEMAN, W.

1904. Coloration in Polistes. Carnegie Inst. Wash., Publ. 19.

FOLSOM, J. W.

1906. Entomology with Special Reference to its Economic and Biological Aspects. Philadelphia.

GORTNER, R. A.

1911. Studies in Melanin. Amer. Nat., 40:743-755.

HORN, GEORGE

1892. Variation in Cicindelidae. Ent. News, 3:25-28.

HORN, W.

1904. Cicindelidae of Ceylon. Spolia Zeylanica, 2:1-16.

1905. Systematischer Index der Cicindeliden. Deutsche Ent. Zeit., Supp. Feb.

Horn, W. (*continued*)

1906. Beitrag zur Erkenntnis der Zeichnungs-Abänderungen bei Cicindeliden. Deutsche Ent. Zeit., 173-174.

1908. Genera Insectorum. Carabidae; Cicindelinae, fasc. 82A.

1910. Ibid., fasc. 82B.

1915. Ibid., fasc., 82C.

Horn, W., and Rosche, H.

1891. Monographie der paläarktischen Cicindeliden. Berlin (published privately).

Leng, C. W.

1902. Revision of the Cicindelidae of Boreal America. Trans. Am. Ent. Soc., 28:93-186.

1912. The Geographic Distribution of Cicindelidae in Eastern North America. Jour. N. Y. Ent. Soc., 20:1-17.

Linden, M. von

1902. Le dessin des ailes des Lépidoptères, recherches sur son évolution dans l'ontogenèse et la phylogenèse des espèces son origine et sa valeur systématique. Ann. sci. nat. zool., (8) 14:1-196.

Mayer, A. G.

1896. The Development of the Wings and Their Pigment in Butterflies and Moths. Bull. Mus. Comp. Zool., 29:209-235.

1897. On the Colors and Color Patterns of Moths and Butterflies. Proc. Bost. Soc. Nat. Hist., 27:243-330.

Michelson, A. A.

1911. On Metallic Colouring in Birds and Insects. Phil. Mag., 554-567.

Packard, A.

1900. Textbook of Entomology, New York.

Riddle, O.

1909. Our Knowledge of Melanin Color Formation and Its Bearing on the Mendelian Description of Heredity. Biol. Bull., 16:316-351.

Shelford, V. E.

1906. Horn's Systematischer Index der Cicindeliden. Jour. N. Y. Ent. Soc., 14:5-9.

1907. Preliminary Note on the Distribution of the Tiger Beetles (Cicindela) and Its Relation to Plant Succession. Biol. Bull., 14:9-14.

1908. Life Histories and Larval Habits of the Tiger Beetles. Linn. Soc. (London) Jour. Zool., 30:157-184.

1911. Physiological Animal Geography. Jour. Morph. (Whitman Volume), 22:551-617.

1912. Ecological Succession, IV. Vegetation and the Control of Land Communities. Biol. Bull., 23:59-99.

1912a. Ecological Succession, V. Aspects of Physiological Classification. Biol. Bull., 23:331-370.

1913. Noteworthy Variations of the Elytral Tracheation of Cicindela. Ent. News, 24:124-125.

1913a. The Life-History of a Bee-Fly (*Spogostylum anale*, Say) Parasite of the Larva of a Tiger-beetle (*Cicindela scutellaris lecontei*, Hald.) Amer. Ent. Soc., 6:213-225.

Shelford, V. E. (*continued*)

1913b. Animal Communities in Temperate America as Illustrated in the Chicago Region. A Study in Animal Ecology. 380 pp. Chicago.

1914. Abnormalities and Regeneration in Cicindela. Amer. Ent. Soc., 8:291-295.

1915. Elytral Tracheation of the Tiger Beetles (Cicindelidae). Tr. Amer. Micr. Soc., 34:241-254.

Tower, W. L.

1903. Origin and Development of the Wings of Coleoptera. Zool. Jahrb., Anat., 17:517-572.

1903a. Colors and Color Pattern of Coleoptera. Dec. Publ. Univ. Chicago, (1) 10:33-70.

1906. An Investigation of Evolution in Chrysomellid Beetles of the Genus Leptinotarsa. Carnegie Inst. Wash., Publ. 48.

Whitman, C. O.

1904. The Problem of the Origin of Species. Cong. of Arts and Sci., Universal Exposition, St. Louis, 5:41-58.

Wickham, H. F.

1902. Habits of American Cicindelidae. Proc. Davenport Acad. Nat. Sci., 7:206-228.

1904. The Influence of the Mutations of the Pleistocene Lakes upon the Present Distribution of Cicindela. Amer. Nat., 38:643-654.

1906. The Races of *Cicindela tranquebarica* Herbst. Ent. News, 17:43-48.

Zeleny, C.

1907. The Direction of Differentiation in Development. The Antennule of *Mancasellus macroyrus*. Arch. Entw. Mech. Org., 23:324-343.

EXPLANATION OF PLATES

Because of the diversity of material studied, the plates of this monograph have been made in different ways and for details and exceptions to the general statements below it will be necessary to see the text. Plates I to IV show camera drawings made chiefly by mounting dry elytra in hot balsam containing little or none of the usual solvents. Plate V is a diagram. Plates VIII to XI were made from specimens killed in the best of fixing fluids and mounted according to approved methods. They represent different individuals chosen at different stages, but have been checked with individual histories. Plates VI, VII, and XII to XXVIII, in so far as they are concerned with elytra, are made up of free-hand drawings of elytra as seen from directly above the center of the curved side, i. e. to the left and above the specimen. The specimens represented are from various sources. All are drawn the same size though the specimens vary greatly. The drawings in plates XII to XVIII are about twice the natural size of an average species. The distribution data shown were supplied from various collections and printed lists. The colored plates which show color ontogeny were made chiefly from the same living individual.

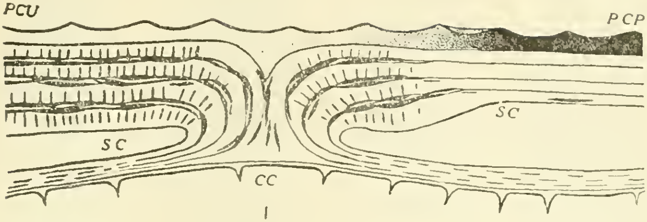
PLATE I

EXPLANATION OF PLATE

FIGURE 1. Cross section of the adult elytron of *C. lepida*, showing the relation of lack of pigment to interlamellar spaces. The portion at the right is through a pigmented area and that at the left through an unpigmented area. *PCU*, primary cuticula, unpigmented; *PCP*, primary cuticula, pigmented; *SC*, secondary cuticula. The portion under the unpigmented areas is divided into layers separated by air-filled spaces above which small canals project into the layer above; under the pigmented part the cuticula is in clear layers with no spaces between. The air spaces in the cuticula under the unpigmented portion are probably the cause of the appearance resembling white pigment in the unpigmented areas.

Figures 2-9. Showing the relation of the markings and tracheae in Cicindela. The tracheae present are from left to right costa *(Co)* (see Fig. 21), the subcosta *(S)*, the radius *(R)*, the media *(M)*, and the cubitus *(Cu)*. The anal cannot ordinarily be demonstrated in dried elytra. The drawings were made with a camera lucida. The figures indicate a number of unpigmented areas which are in the form of cross bands which may be broken by the pigment lying in the lines of the tracheae; the letters *A*, *B*, and *C* indicate the unpigmented stripes to fall between the tracheae.

Fig. 2. *C. regalis* Dej. (Africa); 3, *interrupta* Fabr. (Africa); 4, *interrupta* Fabr. (Africa); 5, *dongalensis* Klg. (N. Africa); 6, *vigintiguttata* Herbst. (India); 7, *compressicornis* Boh. (Africa); 8, *compressicornis* Boh. (Africa); 9, *discrepans* Walk. (Ceylon).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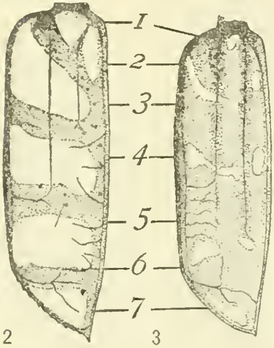

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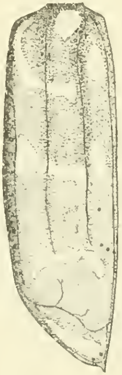

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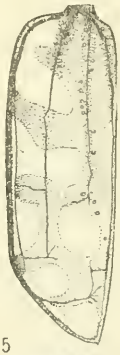

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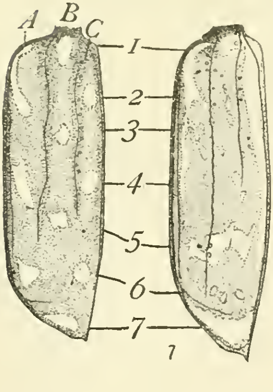
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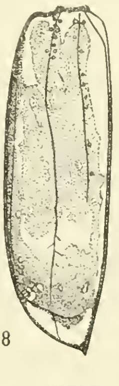

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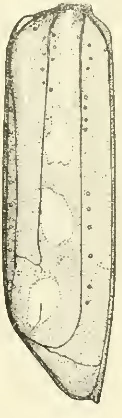

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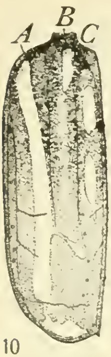
SHELFORD COLORS OF TIGER BEETLES PLATE I

PLATE II

Figures 10-21. Showing the close correlation between the distribution of tracheae and dark pigment in the more specialized patterns of Cicindela. Figures 10 to 22 show close conformation of color patterns and tracheae.

Explanation of Plate

Fig. 10. *C. striolata* Illig. (India) ; 11, *cincta* Oliv. (Africa) ; 12, *anchoralis* Chvr. (S. China) ; 13, *quadrilineata* Fabr. (India) ; 14, *capensis* Linn.—the costa and subcosta were probably present but could not be demonstrated; 15, *capensis* Linn. sub. sp. *chrysographa* Dej. (S. Africa) ; 16, *nivea* Kirb. aber *conspersa* Dej., showing reduction of the media (S. America) ; 17, *pamphila* Lec. (S. U. S.) ; 18, *lugubris* Dej. (Africa) ; 19, *gabbi* G. Horn (S. W. U. S.) ; 20, *dorsalis* Say (Coast of U. S. A.) ; 21, *tenuipes* Dej. (India), *Co,* costa, *S,* subcosta, *R,* radius, *M,* media, *Cu,* cubitus.



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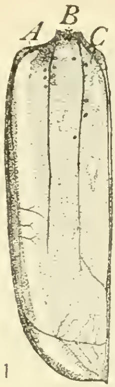

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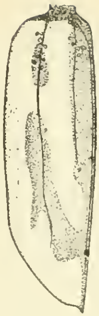

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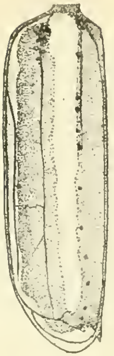

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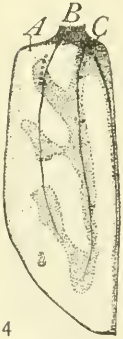

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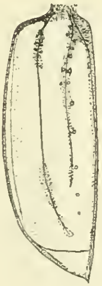

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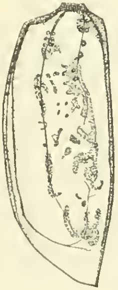

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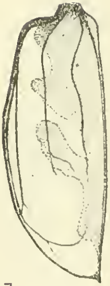

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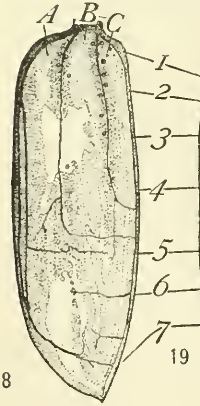
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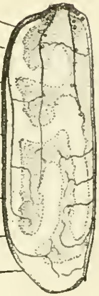

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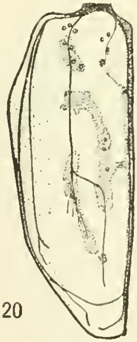

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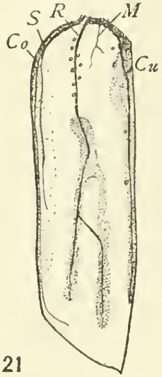

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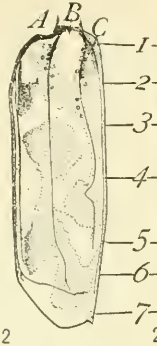
SHELFORD COLORS OF TIGER BEETLES PLATE II

PLATE III

Figures 22-33. Showing the transverse, longitudinal, and oblique bands in Ctenostomidae Collyridae; Cicindelidae (Dromicini and Odontochilini) and variations in the markings of *C. tranquebarica,* a species with typical patterns and variations.

Explanation of Plate

Fig. 22. *C. longipes* Fabr. (Malay Arch.); 23, *imperfecta* Lec. (S. W. U. S.); 24, *luteolineata* Chvr. (Mexico); 25, *lemniscata* Lec. (S. W. U. S.); 26, *Ctenostoma obliquatum* Chd. (South America), showing the central transverse band and distal spot; 27, *Ctenostoma unifasciatum* Dej. (S. America); 28, *Collyris celebensis* Chd. (Malay Arch.), showing three lighter cross bands; 29, *Heptodonta analis* Fabr. (India), showing spots representing two cross bands; 30, *Dromica coarctata* Dej. (S. Africa), showing longitudinal stripes and heavier pigment in the lines of the tracheae; 31-33, showing patterns of *C. tranquebarica* Herbst (N. A.), typical pattern (31) and extended pattern with extensions between the tracheae (32), and a reduced pattern (33) with the middle marking broken in the line of the trachea.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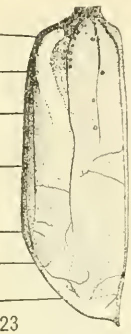

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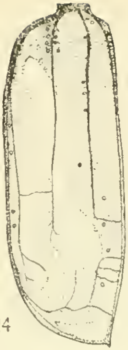

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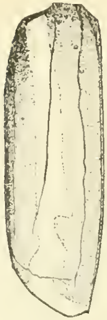

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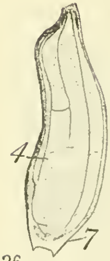

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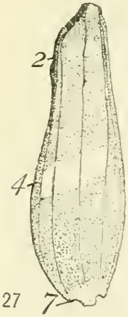

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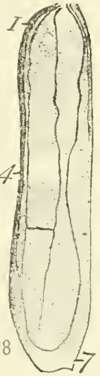

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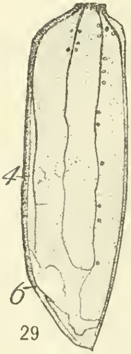

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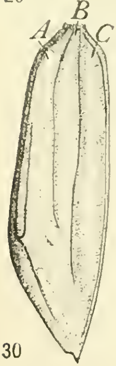

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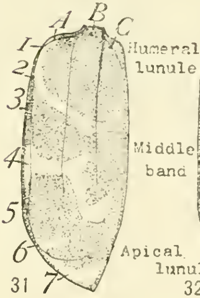
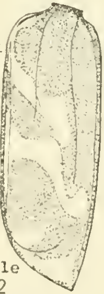

A
B
C
1
2
3
4
5
6
7
Humeral lunule
Middle band
Apical lunule

31



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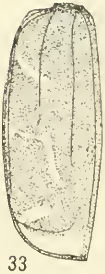


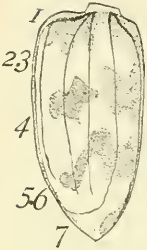
33

PLATE IV

FIGURES 34-38. Showing the relation of the tracheae to pigmentation of the elytra in Carabidae and Dytiscidae.

EXPLANATION OF PLATE

Fig. 34. *Omophron* sp. (N. A.), showing suggestions of transverse bands numbered to correspond with figures 66 and 67 and a tendency for white markings between the bands to lie between the tracheae; 35, *Bembidium versicolor* Lec. (Illinois), showing the unpigmented areas in the lines with the tracheae; 36, unknown carabid (Amazon), showing the pigmented areas in the lines of the tracheae; 37, *Nebia complanata* Linn. (Europe), showing a tendency to lines over the tracheae and between them; 38, *Hydacticus stagnalis* Fabr. (Illinois), showing double lines; 39, *Laccophilus maculosus* Say, showing the transverse bands and suggestion of double unpigmented lines with the tracheae in the pigmented areas (see Fig. 18); 40, *Agabus taeniolatus* Harr. (Illinois), showing trachea in the unpigmented areas with a suggestion of double lines; 41, *Hydroporus undulatus* Say (Illinois), showing the cross bands—a suggestion of all those commonly present in *Cicindela.*



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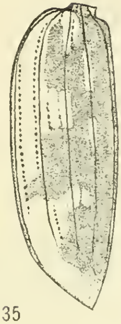

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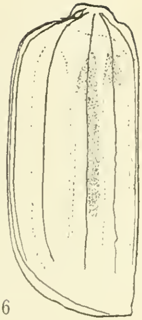

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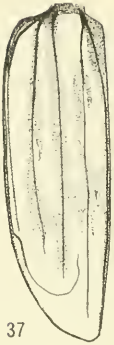

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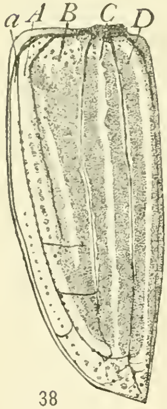

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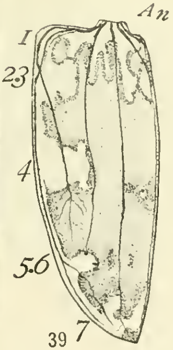

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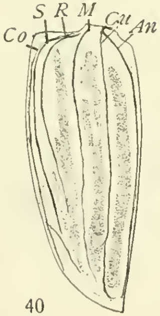

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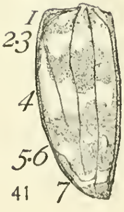


41

SHELFORD COLORS OF TIGER BEETLES PLATE IV

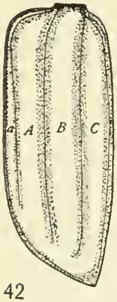
PLATE V

FIGURES 42-49. Showing an analysis of the color patterns of *Cicindela.*

EXPLANATION OF PLATE

Fig. 42. Showing the full number of longitudinal stripes represented in the group—compare with figures 169, 169*a*, and 169*b* (*tetragramma* Boisd.); 43, showing the three longitudinal stripes nearly always represented—compare with 52 (*C. tetragramma,* variation) and 54, *desgodinsi* Fair (Tibet); 44, showing the splitting of the stripes as suggested in 53, *lugubris* Dej. (Africa); 45, showing the full number of cross bands numbered *1* to *7*; 46, showing the commonest cross bands illustrated in 58 (*regalis* Dej. Africa); 47, showing a second common type illustrated by 75, in which none of them reach clear across; 48, showing all the possible spots that can occur from a combination of the longitudinal stripes and cross band shown in figures 42 to 47; 49, showing the spots which are most commonly present or joined to form characteristic patterns in the group.

A and *a* are usually fused on account of the crowding together of the tracheae. The cross bands are never all represented entirely across the elytron, but by dots as in 62, *C. vigintiguttata* Herbst (India). The fusion of *A1, A2* and *B3* gives the characteristic humeral lunule of students of the group, the hook frequently present is made by joining it with *B2*. The fusion of *C1* and *C2* and of *C3* and *C4* gives the characteristic markings shown in the line *C.* of many old world species. The union of *A4, B4* and *B5* gives the characteristic middle band of the group. *A3* is of rare occurrence (see Fig. 198). *A5* is commonly present as a spot, also *A6, B6* and *C6* are less common in occurrence (see Figs. 6 and 7, Pl. I).



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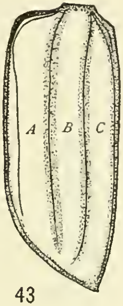

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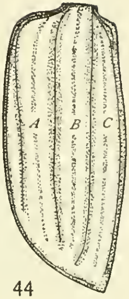

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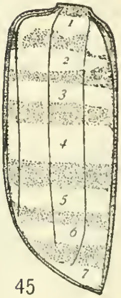

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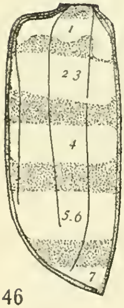

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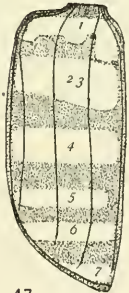

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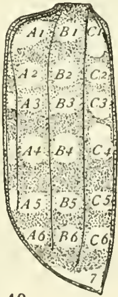
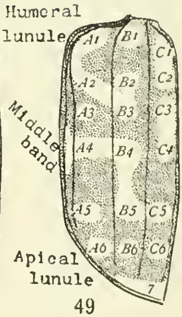

A1 B1 C1
A2 B2 C2
A3 B3 C3
A4 B4 C4
A5 B5 C5
A6 B6 C6
7

48


Humeral lunule
Middle band
Apical lunule
A1 B1 C1
A2 B2 C2
A3 B3 C3
A4 B4 C4
A5 B5 C5
A6 B6 C6
7

49

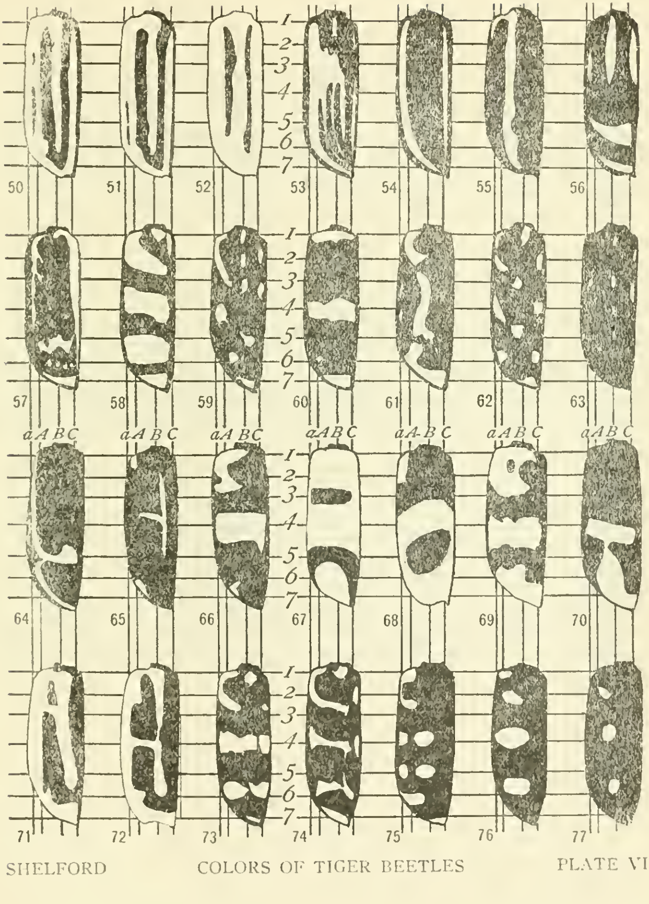
SHELFORD COLORS OF TIGER BEETLES PLATE V

PLATE VI

Figures 50-77. Showing selected Cicindelid patterns with lines to show the correspondence of all the chief types of pattern to the plan shown in Plate V.

Explanation of Plate

Figs. 50, 51, 52, *C. tetragramma* Boisd. (Australia); 53, *lugubrus* Dej. (Africa); 54, *desgodinsi* Fair (Tibet); 55, *interruptofasciata* Schm. (Siam); 56, *muata* sub. sp. *laticornis* Horn (Africa); 57, *compressicornis* Boh (Africa); 58, *regalis* Dej. (Africa); 59, *atkinsoni* Gestro (Australia); 60, *regina* Kolbe (Africa); 61 *melaleuca* Dej. (S. A.); 62, *vigintiguttata* Herbst (India); 63, *notata* Boh (Africa); 64, *gerstaeckeri* Horn (Africa); 65, *Euryoda adonis* subsp. *rufosquata* Bell (Madagascar), Boh; 66, *siamensis,* (Siam); 67, *Odontochila singularis* Flt. (S. A.); 68, *Peridexia hilaris,* Fairm. (Madagascar); 69, *flavosignata,* Cast, (Africa); 70, *crespignyi* Bates (Borneo); 71, *anchoralis* Schm. (China); 72, *copulata* Schm. (India); 73, *interrupta* subsp. *gabonica* Bat. (Africa); 75, *aphrodisia* Baudi (Cypris); 76, *aurulenta* Fabr. (India); 77, *6 punctata,* Fabr. (India).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a A B C
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SHELFORD COLORS OF TIGER BEETLES PLATE VI

PLATE VII

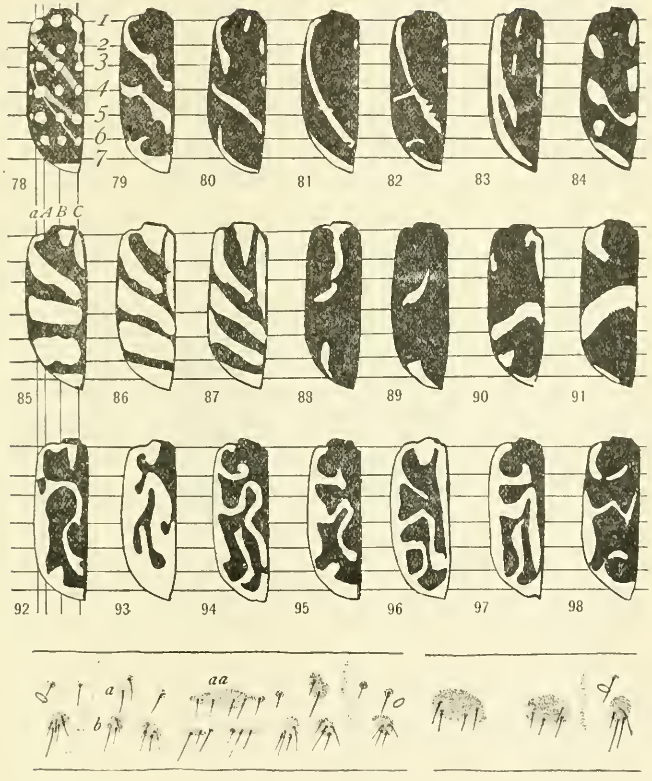
Figures 78-98. Showing some of the chief lines of union of markings not indicated on the preceding chart.

Explanation of Plate

Fig. 78, showing the spots which enter into the patterns with some of the characteristic unions indicated—the stippled areas refer to figures 79 and 80; the narrow white lines to 81, 82, and 83; the dotted lines to 88 and 89, and 90 and 91; 79, *apiata clausseni* Putz (S. A.); 80, *striolata* subsp. *trisignata* Chd. (India); 81, *fatidica* Guer (Africa); 82, *(Prodotes) mimula* Per. (Africa); 83, *viridis* Raffr. (Africa); 84, *peletieri* (N. Africa).

Figs. 85-87. Showing the oblique shifting of the cross markings; 85, *regalis* Dej. (Africa); 86, *andriana* All (Africa); 87, *maheva* Kunck (Africa); 88, *ceylonensis* Horn (India); 89, *oscari* Horn (Africa); 90, *kolbei* Horn (Africa); 91, *princeps ducalis* Horn (India); 92, *longipes* Fabr. (Malay Arch.); 93, *albicans* Chd. (Australia); 94, *nitida* Wdm. (India); 95, *trisignata* Dej. (Europe); 96, *nitidula* Dej. (Africa); 97, *gabbi* S. Horn (S. W. U. S. A.); 98, *leuconoe,* Bates (Mexico).

Figures 99-100. Showing the color areas of the larvae for comparison with figures 101 to 105. Ventral side of the abdominal segment of a larva of *C. tranquebarica.* The areas are lettered as in figure 101; 100, showing the color centers of the dorsal side of a larva. Compare with figure 101. The area with the spiracles is the pleuron.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96
97
98
a
aa
b
o
99
100

SHELFORD COLORS OF TIGER BEETLES PLATE VII

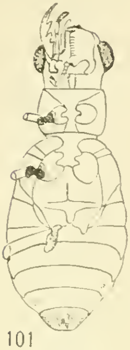
PLATE VIII

FIGURES 101-110. Showing the development of pigment in the legs and body of *C. tranquebarica*, Herbst.

EXPLANATION OF PLATE

Figures 101-110. Showing the pigment beginning at the posterior end of the body and moving forward except the trochanters which are pigmented at emergence; 101, 3 to 6 hours after emergence; 102, 8 to 12 hours; 103, 12 to 15 hours; 104, 24 to 36 hours. *A*, anterior band of pigment on the segment; *f*, the posterior band of the segment; *aa*, the large central anterior area—compare with figure 105.

Figs. 105-108, showing the development of pigment in the dorsal side of the abdomen; 105, at emergence, showing the large dorsal spots beginning of the posterior segments; 105*a*, after 3 to 6 hours, showing the fusion of the spots toward the center; 106, 8 to 10 hours after emergence, showing the nearly complete abdominal pigment, the beginning of the pigmentation of the thorax, and the lines on the head; 107, showing the increase in the head and thoracic regions at 12 to 15 hours after emergence; 108, showing the dorsal side of the head and thorax after 24 to 36 hours; 109 *a* to *d*, the antenna; 3 hours after emergence; *b*, 6 hours after emergence; *c* at 8 to 10 hours after emergence; *d*, 11 to 15 hours after emergence; *e*, 24 hours after emergence; 110, *a*, showing the hind leg three days after emergence; *b*, at emergence; *c*, after 6 to 8 hours; *d*, 12 hours after emergence.



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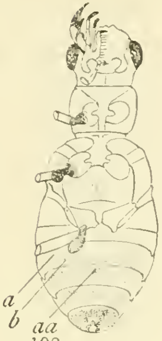

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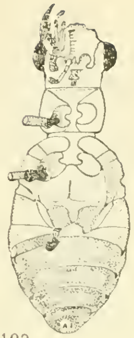

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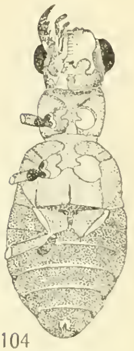

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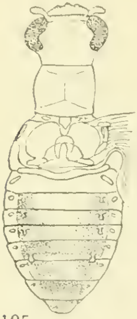
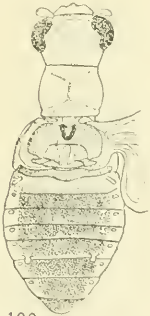


105 *a*



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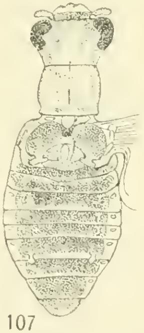

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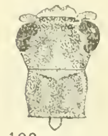

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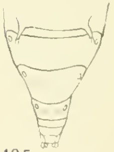

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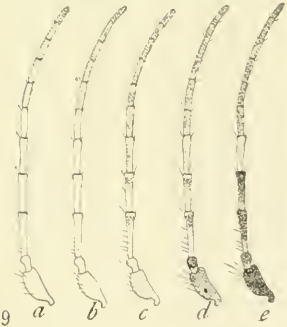

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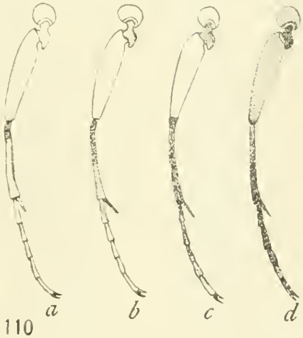


110

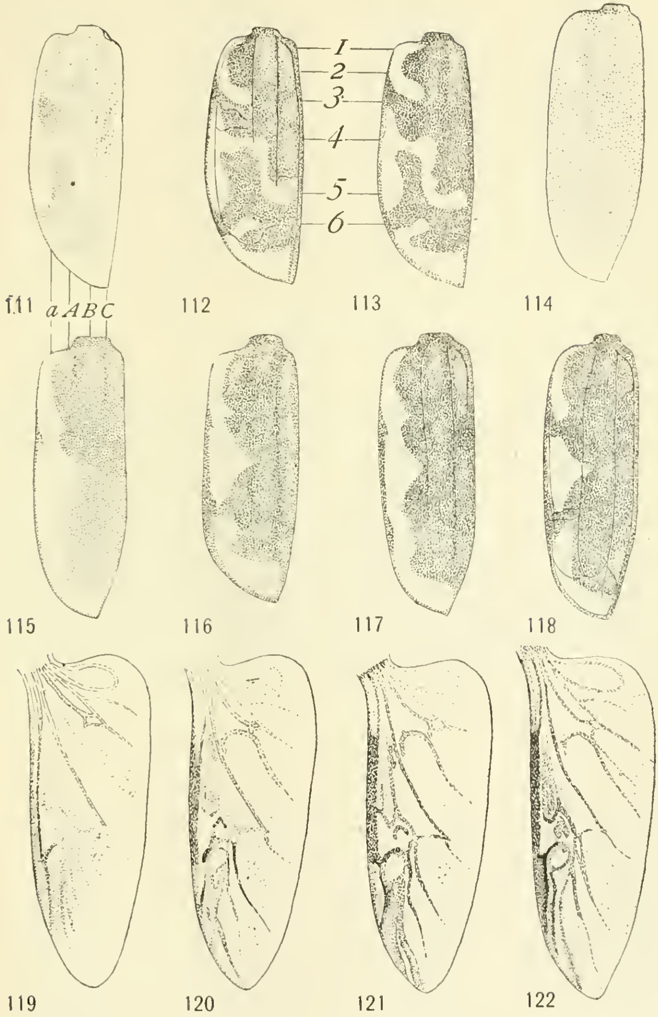
SHELFORD COLORS OF TIGER BEETLES PLATE VIII

PLATE IX

Figures 111-122. Showing stages in the development of pigment in the elytron of *C. repanda* Dej. and *C. scutellaris* aber *lecontei* Hald.

Explanation of Plate

Fig. 111, 4 to 5 hours after emergence, showing the longitudinal lighter areas corresponding to *A, B, C* of the preceding figures; 112, after 12 to 15 hours, showing the stripes *A, B, C* broken into cross bands, *3* and *4* being clearly indicated in the stripe *C;* 114-118, showing stages in the development of the elytral pigment in *C. scutellaris lecontei* Hald; 114, after 4 to 5 hours; 115, after 12 hours, showing particularly a well indicated cross band not appearing in the adult; 116, after 15 hours, showing well marked longitudinal bands broken in spots; 117, after 36 hours with similar marking indicated; 118, after 36 hours, similar to 117; 119, the hind wing at emergence; 120, after 12 hours; 121, after 36 hours; 122, adult.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a
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122

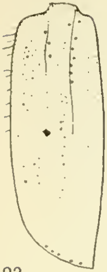
SHELFORD COLORS OF TIGER BEETLES PLATE IX

PLATE X

Figures 123-134. Showing stages in the development of the pigment of the elytra of *C. purpurea limbalis* Klg. (123-130), and in *C. tranquebarica* Herbst (131-134). The wing areas are indicated by letters and numbers as in the preceding figures.

Explanation of Plate

Fig. 123. Three hours after emergence, showing the lighter areas between the tracheae; 124, after 8 hours—suggestion of both longitudinal stripes transverse bands; 125, showing a similar condition after 10 hours; 126, similar conditions at the end of 12 to 15 hours; 127, a similar suggestion of markings at 30 hours; 128, well defined markings at 36 hours; 129, striking longitudinal stripes at 36 hours; 130, heavier pigmentation in the lines of the trachea in the adult; 131 to 134, showing a similar series for the development of pigment in *C. tranquebarica* Herbst; 131, 6 to 8 hours after emergence; 132, 10 hours after emergence; 133, 12 hours after emergence; 134, 24 to 36 hours after emergence.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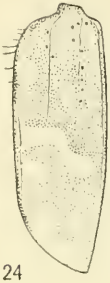
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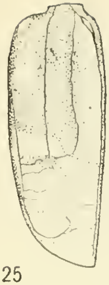
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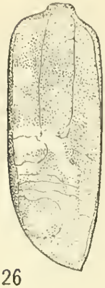
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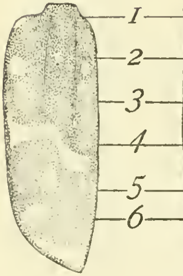

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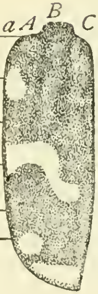

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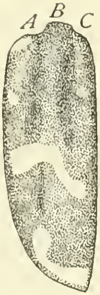

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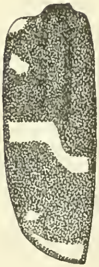
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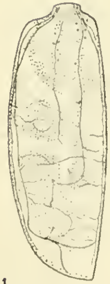
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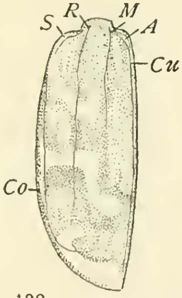

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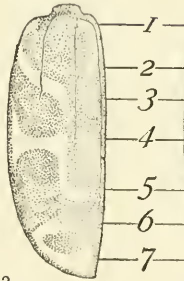

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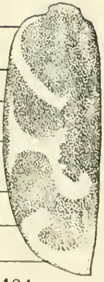
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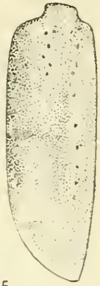
SHELFORD COLORS OF TIGER BEETLES PLATE X

PLATE XI

Figures 135-146. Showing the ontogeny of pigmentation in *C. punctulata* Oliv., *C. sexguttata* Fabr., *Tetracha carolina* Linn., *C. hirticollis* Say, and *C. 12 guttata* Dej.

Explanation of Plate

Fig. 135, *C. punctulata* Oliv. at the end of 6 hours after emergence; 136, after 12 to 13 hours; 137, after 36 hours; 138, *sexguttata* Fabr. after 24 hours; 139, *Tetracha carolina* Linn. at the end of 9 hours after emergence; 140, the adult elytron; 141-145, showing stages in the development of pigment in *hirticollis* Say; 141, 4 hours after emergence; 142, after 6 to 10 hours; 144, after 12 hours; 145, after 16 to 24 hours; 146, *12 guttata,* after 12 to 18 hours.



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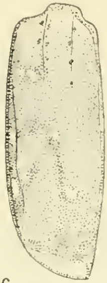

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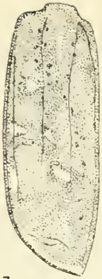

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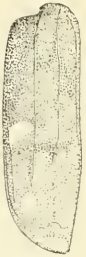

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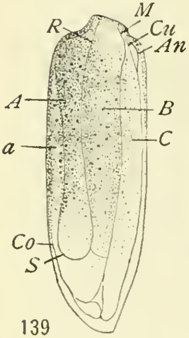
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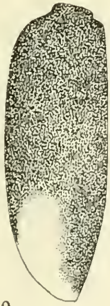

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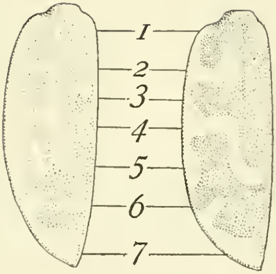

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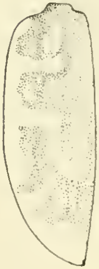

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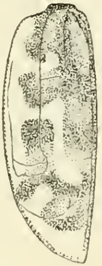

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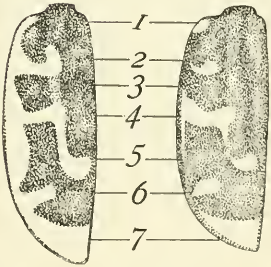

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SHELFORD COLORS OF TIGER BEETLES PLATE XI

PLATE XII

FIGURES 147-187. Showing patterns made up of longitudinal and transverse bands variously broken and contrived. Follow the arrows in tracing out the different directions of modification. For meaning of letters see page 9.

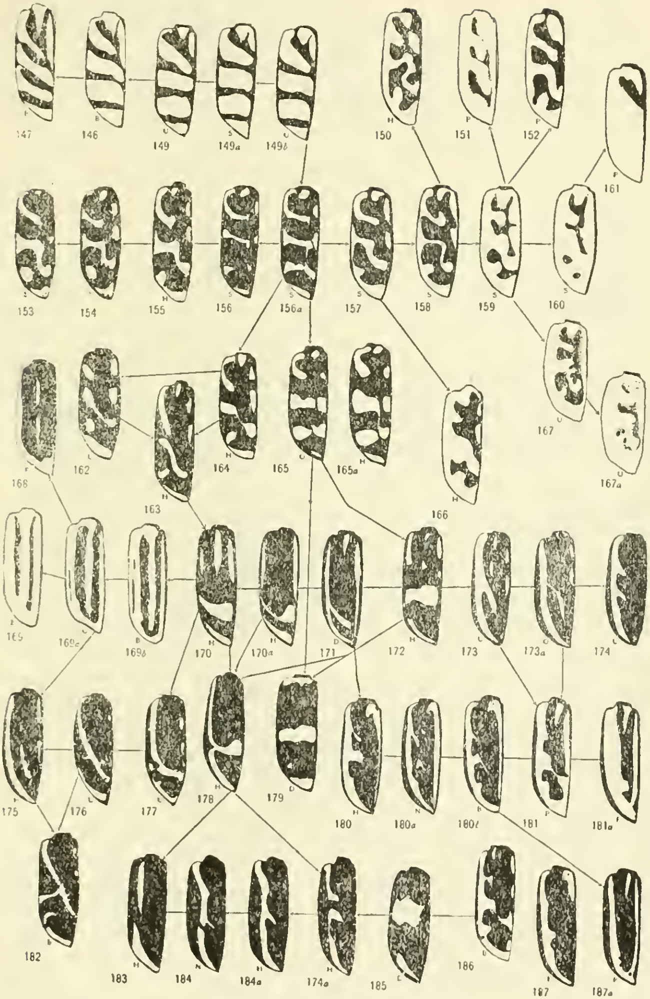
EXPLANATION OF PLATE

Figs. 147-149*B*, showing the typical transverse wide transverse band type of pattern and modifications; 147, *maheva* Kunck. (Madagascar); 148, *andriana* All. (Madagascar); 149, *regalis* Dej. (Africa); 149 *a* and *b*, the same.

Figs. 150-167*a*, showing *interrupta gabonica* type of broken transverse bands and their modification. The patterns of *gabonica* 165 and 165*a* are made up of transverse bands and broken in the lines of the tracheae with various lines of longitudinal and transverse union.

Figs. 150-152, showing the unusual patterns belonging to this group; 150, *singularis* Chd. (N. E. Africa); 151, *kollari* Gistl. (S. Africa); 152, *malaris* Horn (S. A.); 153 and 154, *flexuosa* Fabr. (Europe); 155, *striatifrons* Chd. (India); 156-156*a*, *interrupta* Fabr. (Africa); 157, *monteiroi* Bat. (S. Africa); 158, *brevicollis* subsp. *clathrata* Dej. (Africa); 159-160, *candida* Dej. (Africa); 161, *blanchardi* Fairm. (S. Africa); 162, *peletieri* Luc. (N. Africa); 163, *vittigera* Dej. (India); 164, *multiguttata* Dej. (India); 165, *interrupta* Fabr. subsp. *gabonica* (Africa); 165*a*, *interrupta* Fabr. subsp. *gabonica;* 166, *laetescripta* Mtsch. (E. Asia); 167, *lepida* Dej. (Illinois).

Figs. 168-169*a*, showing pattern with three longitudinal stripes; 168, *queenslandica* Sloane (Australia) (After W. Horn); 169*a*, *tetragramma* Boisd. (Australia); 170-170*a*, *muata* subsp. *laticornis* Horn (Africa); 171, *muata* Horn (Africa); 172, *juno* Horn (Africa); 173, 173*a*, *viridis* Raff (Africa); 174, *gigantea* Raffr. (Africa); 175, *prodotiformis* Horn (Africa); 176, *fatidica* Guer. (Africa); 177, *miseranda* Horn (Africa); 178, *gerstaeckeri* Horn (Africa); 179, *regina* Kolbe (Africa); 180-180*a*, *b*, *mechowi* Lued (Africa); 181-181*a*, *brazzai* Flt. (Africa); 182, *minula* Per. (Africa); 183, *quadristriata* Horn (Africa); 184-184*a*, *petiti* Guer. (Africa); 174*a*, *gigantea* Raffr. (Africa); 185, *junkeri* Kolbe (Africa); 186, *vittata* Fabr. (Africa); 187-187*a*, *congeensis* Flt. (Africa).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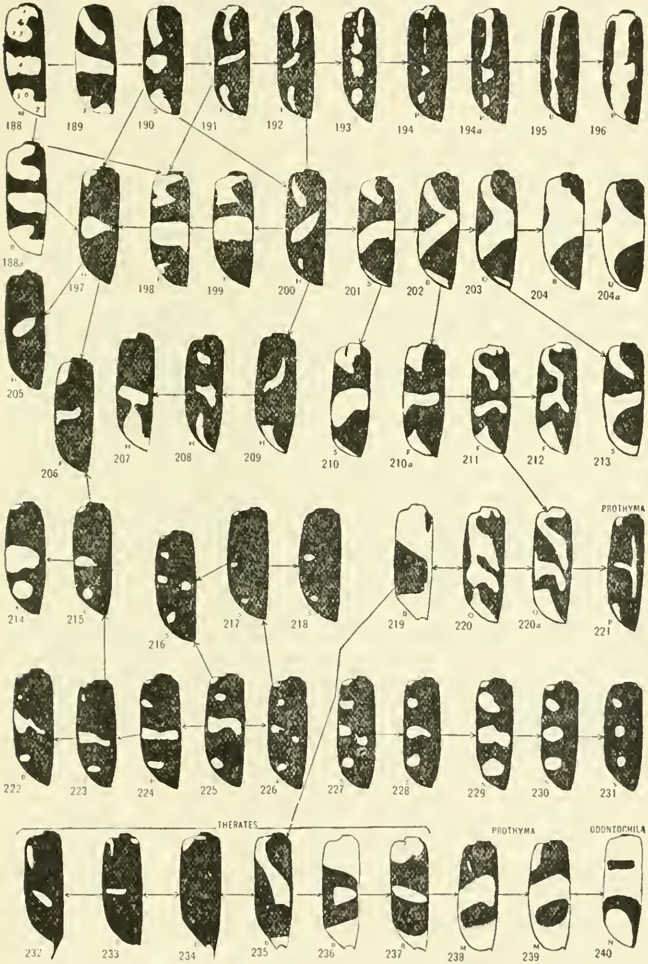
SHELFORD COLORS OF TIGER BEETLES PLATE XII

PLATE XIII

FIGURES 188-240. Showing the domination of the central stripe *(B)*, obliquity in the middle band reversed from the usual type. For meaning of letters see page 9. Follow the arrows in tracing out the different lines of modification. Figures 188 and 188*a* show the reduced transverse bands—compare with 149.

EXPLANATION OF PLATE

Fig. 188 and 188*a*, *C. flavosignata* Cost. (Africa); 184, *dives* Gory, after Gory (India); 190, *aurovittata* Brll. (India); 191, *ceylonensis diversa* Horn, after Horn (India); 192, *ceylanensis* Horn, after Horn (India); 193, *discrepans* Wak (India); 194 and 194*a*, *harmandi* Flt. (India); 195, 196, *interruptofasciata* Schm. (India); 197, *assamensis* Parry (India); 198-199, *siamensis* Flt. (India); 200, *andrewesi mauritti* Horn (India); 201, *princeps ducalis* Horn (India); 202, *aurofasciata* Dej. (India); 203, *aurofasciata* Dej. (India); 204-204*a*, *aurofasciata lepida* Gory (India); 206, *assamensis* ?; 207, *crespignyi* Bat. (Malay Islands); 208, *kachovskyi* Horn (Africa); 209, *oskari* Horn (Africa); 210-210*a*, *shivah* Parry (India); 211-212 (After Schaum), *calligramma* Schm. (India); 213, *aurofasciata* Dej. (India); 214, *haemorrhoidalis* Wdm. (India); 215, *burmeisteri* Fischer (Asia); 216, *stenodora* Schm. (Malay Arch.); 217, *minuta* Oliv. (India); 218, *craspedota* Schm. (Borneo); 219, *semperi* Horn (India); 220, *calligramma* Schm. (India); 221, *Prothyma adonis rufosignata* Brll. (Madagascar); 222, *chinensis japonica* Thnb. (Japan); 223, *chinensis* DeG. (China); 224, *duponti* Dej. (India); 225, *exima* Vand. (Malay Arch.); 226, *ferriei* Flt. (Japan); 227, *didyma* Dej. (Malay Arch.); 228, *aurulenta* Fabr. (India); 229, *notata* Wdm. (India); 230, *aurulenta* Fabr. (India); 231, *punctata* Fabr. (India); 232, *Therates whiteheadi* Bates (Malay Arch.); 233, *T. fruhstorferi* Horn (Tonkin); 234, *T. spinipennis* Latr. and Dej. (Malay Arch.); 235, *T. chaudoiri* Schm. (Malay Arch.); 236, *T. maindroni* Horn (Malacca); 237, *T. crinys* Bates (Malay Arch.); 238, *Peridoxia hilaris* Fair. (Madagascar); 239, *Peridaxia fulvipes* Dej. (Madagascar); 240, *Pometon singularis* Flt. (S. A.).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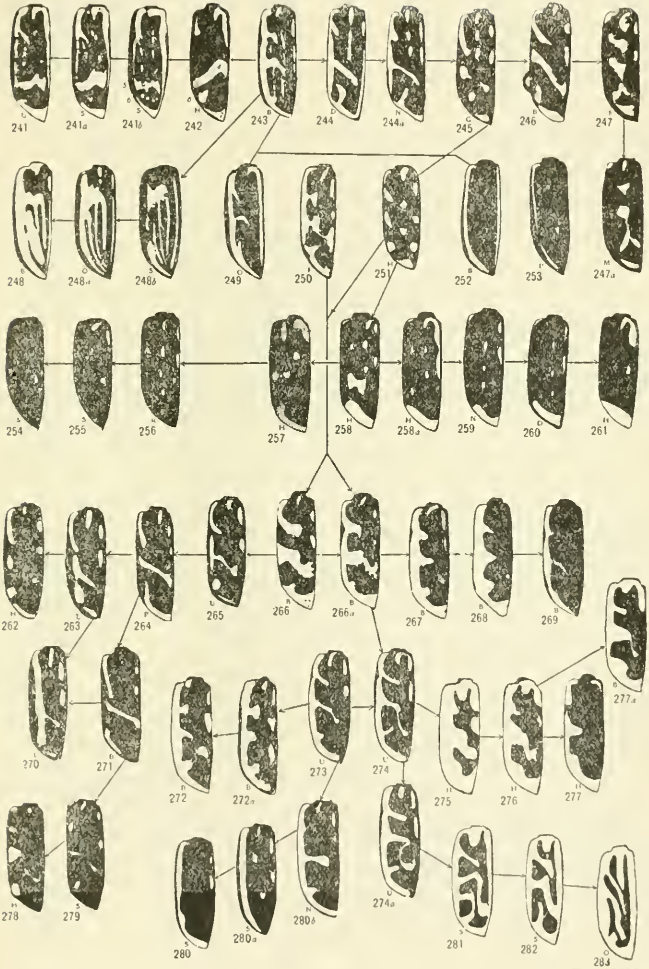
SHELFORD COLORS OF TIGER BEETLES PLATE XIII

PLATE XIV

Figures 241-283. Showing patterns made up of numerous spots and stripes. Figures 241 to 243 and 248, 248*a*, and 248*b* should be compared with plate IV, figure 38. In comparing the figures follow the arrows. For meaning of letters see page 9.

Explanation of Plate

Figs. 241-241*a*, *b*, *C. compressicornis*, Beh. (Africa); 242, *kolbei* Horn (Africa); 243, *deyrollei* Guer. (Africa); 244, *maino* Gestro (N. Guinea); 245, *atkinsoni* Gestro (India); 246, *feisthameli* Guer. (Africa); 247 (after Guerin)-247*a*, *nysa* Guer. (Liberia); 248, 248*a*, 248*b*, *lugubris* Dej. (Africa); 249, *deyrollei* Guer. (Africa); 250, *vittata* Fabr., after Guerin (Africa); 251, *20 guttata* Herbst (India); 252, *desgodinsi* Fair. (Tibet); 253, *latreillei* Guer. (Kapaur)—the stippled spots are dark and represent areas in which spots usually occur; 254-255, *rasticana* Per. (S. Africa); 256, *notata* Boh. (S. Africa); 257, *latreillei* Guer. (Kapaur); 258-258*a*, *b*, *rasticana* Per. (S. Africa); 259, *rasticana* aber *egregia* Per. (S. Africa); 261, *bioncani* subsp. *liengmei* Per. (S. Africa); 262-263, *striolata* Ill. (Burmah); 264, *striolata* subsp. *trisignata* Chd. (Timor); 265, *neumanni* Kolbe (Africa); 266, *pudica* Boh. (Zulu); 266*a*, Boh. (Transvaal); 267-268, *escheri* Dej. (S. Africa); 269, *marginella* Dej. (Africa); 270, *striolata* Ill. (India); 271, do subsp. *trisignata* Chd. (Timor); 272, *luxeri* Dej. (Africa); 273, *heros* Fabr. (Malay Arch.); 274-274*a*, *heros* Fabr. (Malay Arch.); 275-277*a*, *monteiroi* Bat. (Africa); 278-279, *strachani* Hope (Africa); 280-280*a*, *b*, *equestris* Dej. (Madagascar); 281, *nitidula* Dej. (Africa); 282, *nilotica* Dej. (Africa); 283, *albina* Wdm. (India).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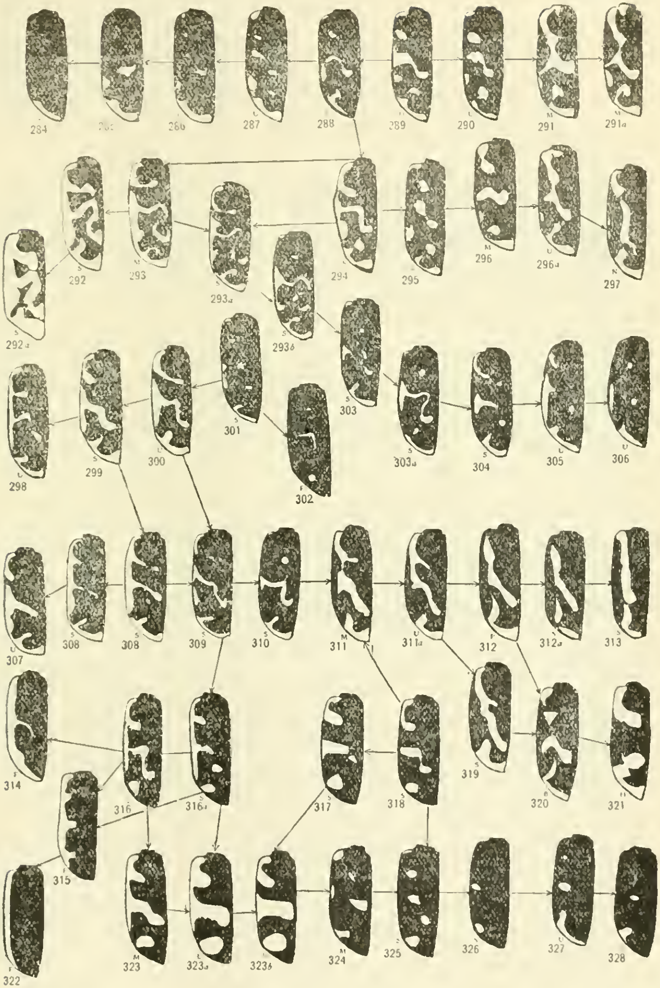
SHELFORD COLORS OF TIGER BEETLES PLATE XIV

PLATE XV

FIGURES 284-328. Showing the patterns of North American species belonging chiefly to the Mexican and *C. argentata* groups and having cross bands *5* and *6* both distinctly represented in the majority. For meaning of letters see page 9. Various combinations of spots which go to make up the oblique vitta of some of the species of the group are represented in figures 291, 296, 297, 311, 312, 313, 319, and 320; compare these with figures 23 and 24 and 78 to 82.

EXPLANATION OF PLATE

Fig. 284, *C. polita* Lec. (Texas); 285, *abdominalis* Fabr. (Atlantic coast, U. S.); 286, *rufiventris* aber. *cumatilis* Lec. (Texas); 287, *rufiventris* Dej. (Eastern U. S.); 288, *16 punctata* Klg. (N. Mex.); 289, *carthagena* subsp. *hentzi* G. Horn (Mass.); 290, *16 punctata* Klg. (Mexico); 291-291*a*, *rufiventris* aber. *mellyi* Chd. (Mexico); 292, *trifasciata* Fabr. (S. A.); 293-293*a*, *b*, *trifasciata* subsp. *sigmoidea* Lec. (S. U. S.); 294, *carthagena* Dej. (Mexico); 295, *rufiventris* subsp. *16 punctata* Klg. (Mexico); 296, *rufiventris* aber *mellyi* Chd. (Mexico); 297, *melaleuca* Dej. (S. A.); 298, *obsoleta* Say (S. W. U. S.); 299, *fera* Chv. (Mexico); 300, *pusilla* subsp. *cinctipennis* Lec. (S. W. U. S.); 301, *punctulata* Oliv. (U. S. and Mex.); 302, *argentata* subsp. *aureola* Klg. (S. A.); 303-303*a*, *argentata* Fabr. (Brazil); 304, *lunalonga* Schm. (California); 305, *celeripes* Lec. (Central U. S.); 306, *cursitans* Lec. (Miss. Valley); 307, *schaupii* G. Horn (Texas); 308-308*a*, *nephelota* Bat. (Mexico); 309-309*a*, *chlorostricta* subsp. *staudingeri* Horn (S. A.); 310, *argentata* subsp. *venustula* Gory (Mexico); 311-311*a*, *pusilla* subsp. *imperfecta* Lec. (Pacific States); 312, *luteolineata* Chvr. (Mexico); 313, *lemniscata* Lec. (Arizona); 314, *debilis* Bates, after Bates (Mexico); 315, *favergeri* Brll., after Andouin and Brullé (S. A.); 316, 316*a*, 317, *raseiventris* Chvr. (Mexico); 318, *flavopunctata* Chvr. (Mexico); 319, *pusilla* subsp. *imperfecta* Lec. (Pacific States); 320, *craveri* Thms. (Mexico); 321, *marquardti* Horn—the only Cicindelid without a middle band (Sao Paulo); 322, *hoegei* Bat. after Bates (Mexico); 323-323*a*, *b*, *sommeri* Mann. (Mexico); 324, *anulipes* Horn (S. A.); 325, *flavopunctata* Chvr. (U. S. and Mexico); 326, *chrysippe* Bates (Mexico); 328, *severa* Laf. (Gulf States and N. M.); 328, *striga* Lec. (Florida).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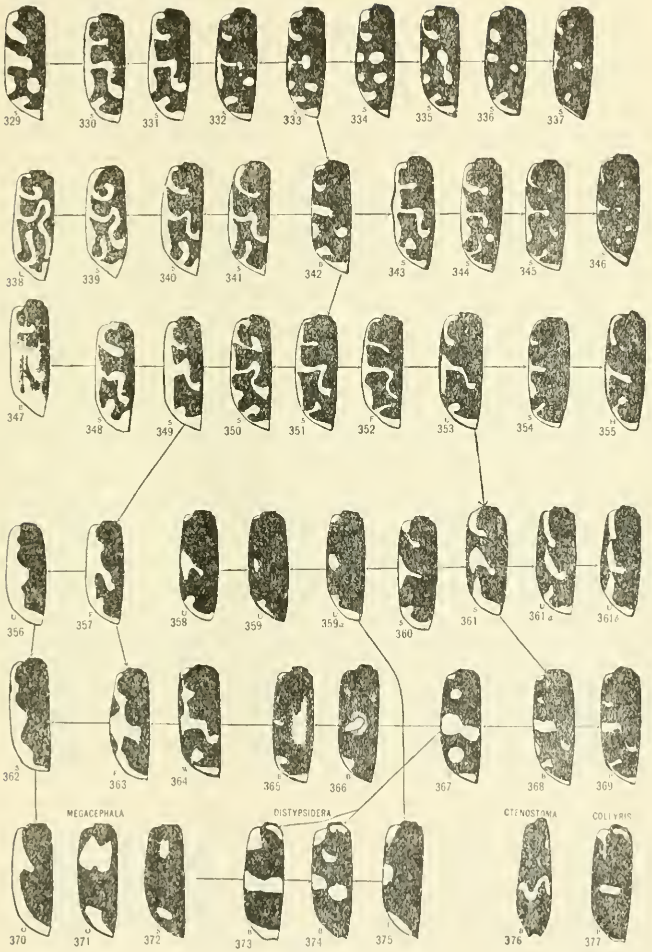
SHELFORD COLORS OF TIGER BEETLES PLATE XV

PLATE XVI

FIGURES 329-377. Showing the patterns of the principal Eurasian species exclusive of the *flexuosa* and *longipes-biramosa-limosa* (Oriental) groups, with a few representative patterns from the genera Megacephala, Distypsidera, Ctenostoma, and Collyris. For meaning of letters see page 9. Figures 330-332 are related American species. Figures 329-355 show the typical and characteristic patterns of the genus Cicindela in which the portion of the elytron nearest the scutellum is without spots, in which bands *2* and *3* are fused and *5* and *6* are separate, and the modifications of the same.

EXPLANATION OF PLATE

Fig. 329, *C. donegalensis* Klg. (Africa); 330, *hirticollis* Say (Illinois); 331, *repanda* Dej. (Illinois); 332, *12 guttata* Dej. (Illinois); 333, *lunulata* Fabr. (Europe); 334, *aphrodisia* Baudi (Cypris); 335, *lacrymosa* Dej. (Japan); 336, *10 guttata* Fabr. (Malay Arch.); 337, *discreta* Schm. (Malay Arch.); 338, *nitida* Wdm. (India); 339, *contorta* Fisch. (Europe); 340, *trisignata* Dej. (Europe); 341, *litterifera* Chd. (Europe); 342, *alboguttata* Klg. (Arabia); 343, *sumatrensis* Herbst (India); 344-345, *orientalis* Dej. (Europe); 346, *melancholica* Fabr. (Europe and Africa); 347, *3 signata* aber *subsuturalis* Souv. (Europe); 348, *circumdata* Dej. Europe); 349, *circumdata* Dej. (Europe); 350, *angulata* Fabr. (India); 351, *sumatrensis* Herbst. (Oriental Region); 352, *despecata* Horn, after Horn (Madagascar); 353, *ancosisconensis* Harris (New York); 354, *funerea* subsp. *opigrapha* Dej. (New Guinea); 355, *variolosa* Blanch. (Salathy); 356, *galathea* Thiem. (Asia); 357, *lyoni* Vig., after Roske (Europe); 358, 359, 359*a*, *germanica* Linn. (Europe); 360, *atrata* Pall. (Europe and Asia); 361, 361*a*, *b*, *germanica* subsp. *obliquefasciata* Ad. (Europe); 362, *lacteola* Pall. (Asia); 363, *geminata* subsp. *potanini* Dok., after W. Horn (Tibet); 364, *purpurea* subsp. *limbalis* Klg. (Illinois); 365, *campestris*, showing an unusual light area—the stippled portions are dark areas with cuticula such as covers the lighter spots; 366; *ismenia* Gory—stippled areas as in 365; 367, *maura* Linn. (Europe); 368-369, *fischeri* Adams (Europe); 370, *Megacephala australasiae humeralis* McL. (N. W. Australia); 371, *quadrisignata* Dej. (N. Africa); 372, *M.* (Styphloderma) *asperata* Wat. (Africa); 373, *Distypsidera flavipes* McL. (Australia); 374, *D. gruti* Pasc. (Australia); 375, *Nickerlea distypsideroides* Horn, after Horn (Australia); 376, *Ctenostoma maculicorne* Chvr. (Mexico); 377, *Collyris frushtoferi* Horn (Tonkin).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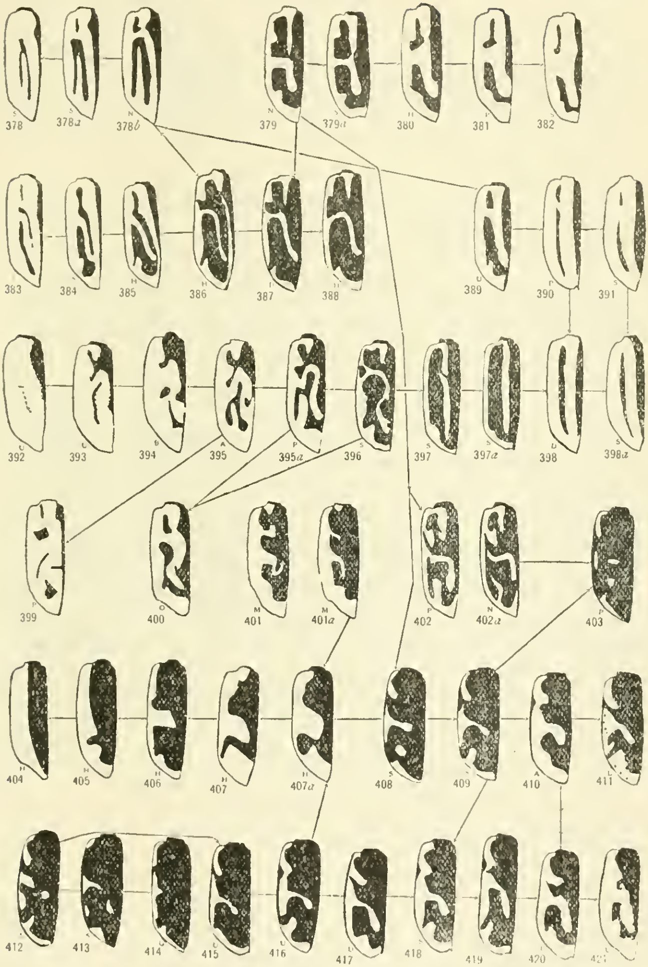
SHELFORD COLORS OF TIGER BEETLES PLATE XVI

PLATE XVII

FIGURES 378-421. Showing the patterns of the characteristic groups of species belonging to the Oriental and Australian Regions. For meaning of letters see page 9. They are in general of a character such as is commonly designated as specialized but show some unusual combinations of areas which tend to confirm the general interpretation here presented.

EXPLANATION OF PLATE

Figs. *378-378a, b, C. arancipes* Schm. (Borneo); *379-379a*, *copulata* Schm. (India); 380, *anchoralis* subsp. *punctatissima* Schm. (China); 381-382, *ornata* Flt. (India); 383, 384, 385, *psammodroma* Chvr. (China); 386, 387, 388, *anchoralis* subsp. *punctatissima* Schm. (China); 389, *anchoralis* Chvr. (China); 390-391, *quadrilineata* subsp. *renei* Horn (India); 392-393, *ypsilon* Dej. (Australia); 394, *rafflesia* Chd. (Australia); 395-395*a*, *albicans* Chd. (Australia); 396, *longipes* Fabr. (Malay Islands); 397-397*a*, *4 lineata* Fabr. (India); 398, 398*a*, *4 lineata* subsp. *renei* Horn (India); 399, *singularis* Chd. (Nubia); 400, *longipes* Fabr. (Malay Islands); 401-401*a*, *wapleri* Lec. (Louisiana); 402-402*a*, *mucronata* Jord. (Malay Islands); 403, *pupilligera* Schm. (New Guinea); 404, *limbata* Schm. (India); 405, *maindroni* Horn (India); 406, *biramosa* Fabr. (India); 407, *bellana* Horn (India); 408,*funerata* subsp. *barbata* Horn (New Guinea); 409, *tuberculata* Fabr. (Australia); 410, *tuberculata* aber *latecincta* White (New Zealand); 411, *parryi* White (New Zealand); 412-413, *10 guttata* Fabr. (New Guinea); 414, *mastersi* McL. (Australia); 415, *feredayi* Bates (New Zealand); 418, *tuberculata* Fabr. (New Zealand); 419, *dunedensis* aber *wakefieldi* Bates (New Zealand); 420, *feredayi* Bates (New Zealand); 421, *perhispida* Brn. (New Zealand).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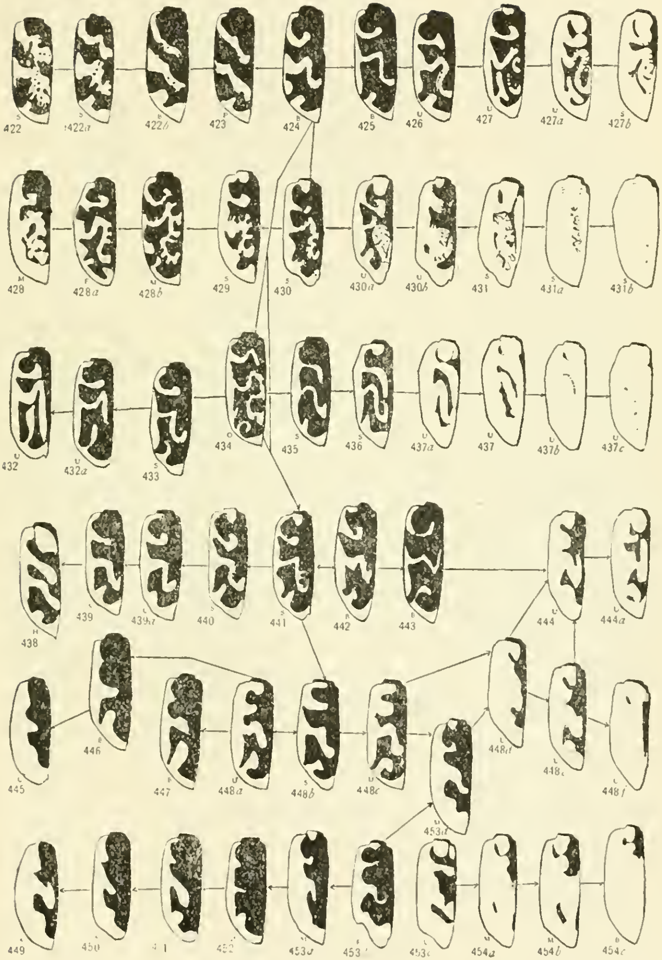
SHELFORD COLORS OF TIGER BEETLES PLATE XVII

PLATE XVIII

FIGURES 422-455. Showing the highly specialized patterns of the South American species belonging chiefly to the *cuprascens* and *argentata* groups of species. For meaning of letters see page 9. All the types have representatives in which pigment has almost entirely disappeared as a rule and there is a strong tendency for the area of the media trachea to degenerate along with the reduction of that treachea (see figures 16 and 20).

EXPLANATION OF PLATE

Figs. 422-422*a, b, C. apiata* Dej. (S. A.); 423, *apiata* aber *clausseni* Putz. (S. A.); 424, *gormazi* Reed. (Chili); 425, *mixta* Horn (Ecuador); 426, *trifasciata* Fabr. (S. A.); 427-427*a, b, graphiptera* Dej. (S. A.); 428-428*a*, after Chevrolot 428*b*, *patagonica* subsp. *cherubim* Chvr. (S. A.); 430-430*a, b, marginata* Fabr. (Texas); 431-431*a, b, nivea* Kirby (S. A.); 430-432*a, gabbi* G. Horn (California); 433, *trisignata* Dej. (Asia); 434, unidentified species from Arica, Peru, in the Oxford University Museum; 435, *curvata* Chvr. (Mexico); 436, *dorsalis* aber *saulcyi* Guer. (Texas); 437-437*a, b, c, dorsalis* Say (Mass.); 438, *malaris* Horn (Pebas, Amazons); 439-439*a, nevadica* var. *knausi* Leng (Kansas); 440, *cuprascens* Lec. (Illinois); 441 *hamata* Brll. (Mexico); 442, *chlorocephala* Chv. (Vera Cruz, Mex.); 443, *leucohoe* Bat. (Mexico); 444, *macronema* Chd. (Mexico); 445, *togata* Laf. (Texas); 446, *auraria* Klg. (S. A.); 447, *boops* (West Indies); 448, *macronema* Chd. (Mexico); 449, *pamphila* Lec. (Texas); 450, *togata* Lec. (Texas); 451, *californica praetexta* Lec. (Texas); 452, *marginata* Fabr. (Texas); 453*a, b, c, d, wapleri* Lec. (Louisiana).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439a
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453d
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448e
448f
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453a
453b
453c
454a
454b
454c

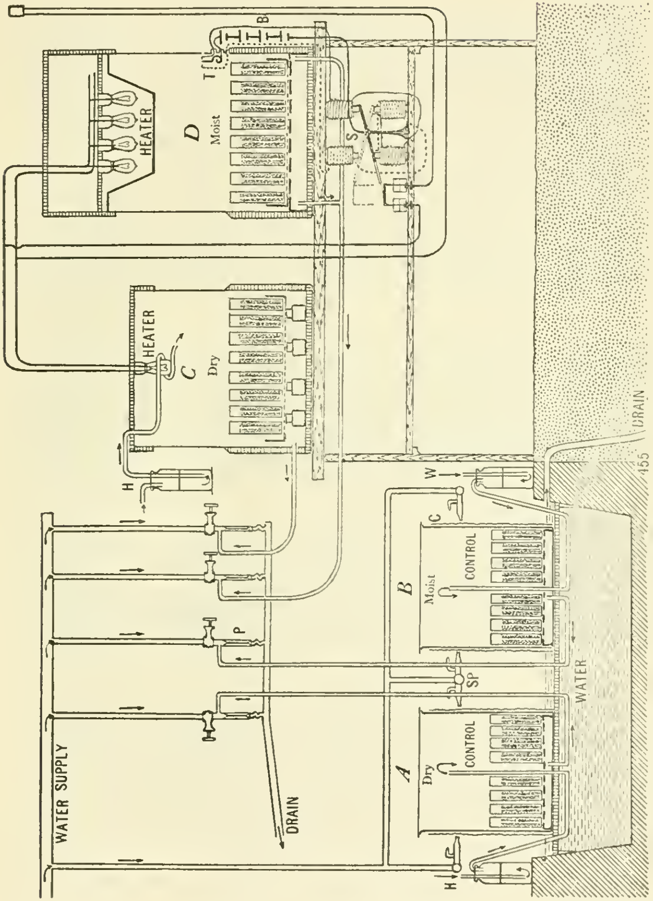
SHELFORD COLORS OF TIGER BEETLES PLATE XVIII

PLATE XIX

Explanation of Plate

Figure 455. Showing the equipment used in the experiments on modification of tiger beetle color and color patterns.

The experiments were conducted in four chambers; two, A and B, which were of galvanized iron, rested with their bottoms in a concrete tank of running water. Trey were wrapped with cheese cloth and sprayed with jets of water on two sides which kept the mean temperature at 21° C. throughout the summer. The other two, C and D, were heated from above with electric lights, blackened in C and separated from the main chamber by a copper jacket in D. These were were heated to a point 10° C. above the temperature of the greenhouse except during the middle of the day. The switch shut off the heat at about 35° C. air temperature and the sun continued to heat the chamber so that the maximum soil temperature sometimes reached 40° C. or more by midafternoon. Air was drawn through the tanks by filter pumps and, in the case of the control tanks, through sulfuric acid for the dry one and water for the moist one, but this intake was not maintained for the high temperature tanks at all times because of mechanical difficulties. The moisture in the moist chambers was maintained by frequent additions of water to the soil, while in the dry chambers as little water as possible was added. *H*, sulphuric acid bottles; *S*, mercury switch; *T*, thermostat; *B*, batteries; *W*, water bottles; *SP*, spray nozzles; *C*, cloth cover.


HEATER
D
Moist
T
B
S
HEATER
C
Dry
H
WATER SUPPLY
DRAIN
P
SP
B
Moist
CONTROL
A
Dry
CONTROL
C
W
H
WATER
DRAIN
455

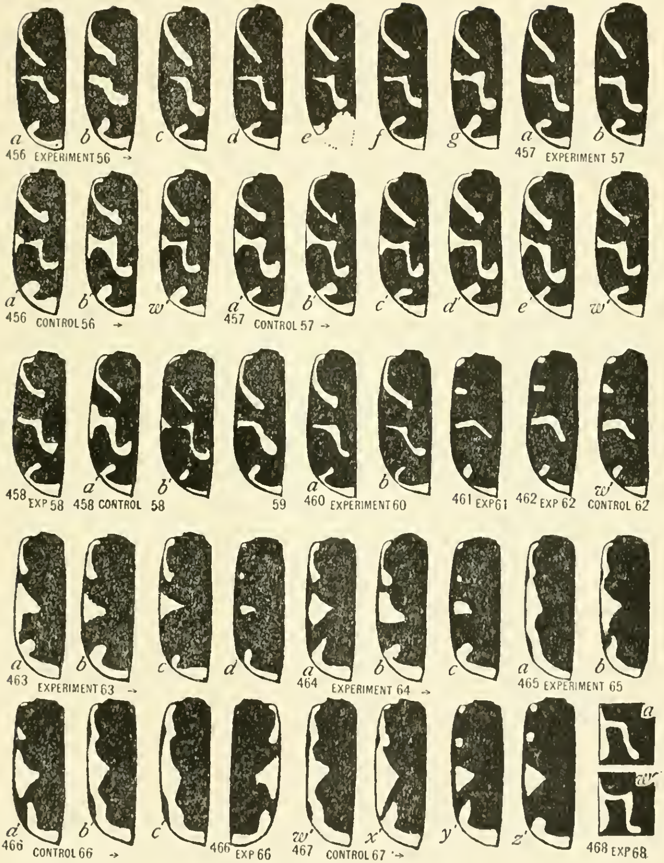
SHELFORD COLORS OF TIGER BEETLES PLATE XIX

PLATE XX

FIGURES 456-465. Showing the color patterns of specimens of *C. tranquebarica* Herbst., *C. purpurea limbalis* Klg., and *C. scutellaris lecontei* Hald. subjected to high temperature under moist and dry conditions and placed in an ice box during their prepupal and pupal life. With them are shown controls which were kept at normal temperatures or lower and designated with letters *a′*, *b′*, etc., and a few collected from the normal habitat from the same generation, designated *w′*.

EXPLANATION OF PLATE

Fig. 456*a-g*, the elytra of seven specimens of *C. tranquebarica* which passed the late larval, prepupal, and pupal stages in a warm moist chamber; mean temperature of the soil, 37° C.; maximum for the warmest week, 40° C.; control, 456*a′*, *b′*, *w′*, at 21° (Experiment 56); 457*a-b*, the elytra of two specimens of *C. tranquebarica*, which passed the late larval, prepupal, and pupal stages in a warm dry chamber, mean temperature 40° C.; control, 457*a′-e′-w′* at 21° C. (Experiment 57); 458, the same as 457 but dry instead of moist; 458*a′-b′* control of the same (Experiment 58); 461, the same moist warm treatment as described under 456 applied to *C. purpurea limbalis*; 462, the same as 461 but dry instead of moist; for normal patterns see figure 512, plate XXVIII; a collected specimen from the same generation showing the extreme type of cross band reduction and forward curvature found either in the controls or the collections from the habitata; 459, showing the pattern of a specimen of *C. tranquebarica* which was forced through its transformations in the fall by a temperature of 37° C. beginning October 1, so that there was no hibernation. This specimen was one emerged early in December. The others emerged in June but none of them showed any modification; 460*a-b*, the same treatment as 456 but dry instead of moist (Experiment 60); 463, showing the patterns of specimens of *C. scutellaris lecontei* Hald. subjected to conditions similar to those mentioned for figure 456; 463*d* shows markings reduced below anything ever collected near Chicago or produced in the controls (Experiment 63); 464*a*, *b*, *c*, showing the patterns of elytra of *C. scutellaris lecontei* subjected to mean temperature of 39° C. under very moist conditions (Experiment 64); 465*a*, *b*, *c*, showing the elytral patterns of two specimens of *C. scutellaris lecontei* Hald. kept in an ice box during the pupal and prepupal stages; 10 to 12° C. from July 20 to September 3; 16 to 20° September 3 to October 16; 466 shows the elytron of a specimen kept at a mean temperature of 40° C., moist; 466*a′*, *b′*, *c′* are the control of the same kept at 21° C.; 467*w′*, *x′*, *y′*, *z′* show elytra of specimens collected in the habitat from which the experimental material came, selected to show the range of variation; 468*a* and *w′* . . *a* shows the middle band of a specimen of *C. hirticollis* showing the rounded angle, transverse portion perpendicular to the inner border of the elytron and the hooked portion at the end rounded—compare with the normal shown in 468*w′*.


a
b
c
d
e
f
g
a
b
456 EXPERIMENT 56 →
457 EXPERIMENT 57
a'
b'
w'
a'
b'
c'
d'
e'
w'
456 CONTROL 56 →
457 CONTROL 57 →
458 EXP 58
a'
458 CONTROL 58
b'
59
a
460 EXPERIMENT 60
b
461 EXP 61
462 EXP 62
w'
CONTROL 62
a
b
c
d
463 EXPERIMENT 63 →
a
b
c
464 EXPERIMENT 64 →
a
b
465 EXPERIMENT 65
d'
b'
c'
466 CONTROL 66 →
466 EXP 66
w'
x'
y'
z'
467 CONTROL 67 →
a
w'
468 EXP 68

SHELFORD COLORS OF TIGER BEETLES PLATE XX

PLATE XXI

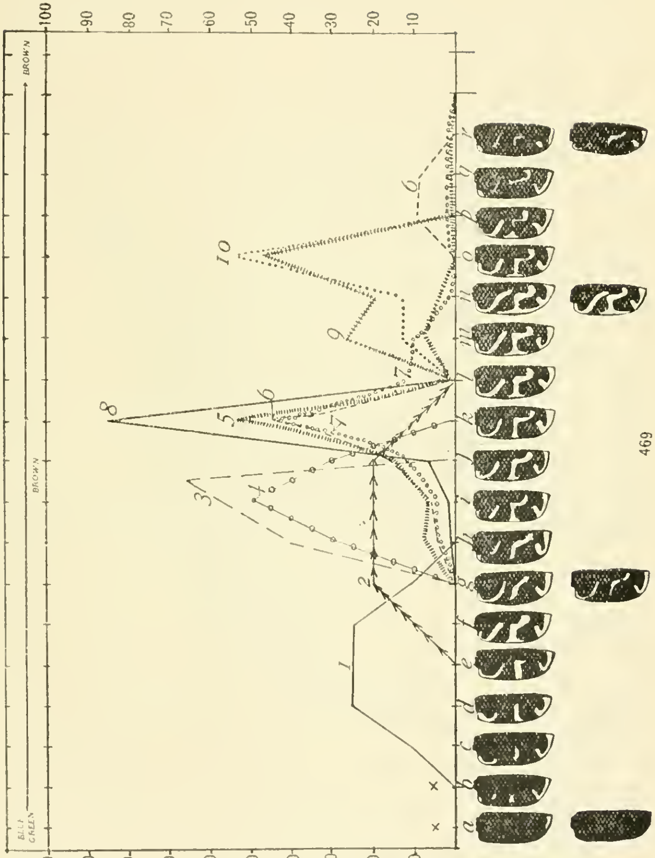
Explanation of Plate

Figure 469. Showing the range of variation in the group of races included under the name *tranquebarica* Herbst. The classes of patterns are arranged in a series *a, b, c, d, e, f,* etc., from left to right and the percentage of individuals in each class for several localities is graphically represented. At the top is indicated the color of the elytra to which the patterns belong but these do not fall in the same classes as the patterns. The graphs are numbered and the localities which they represent are numbered on figure 469*a*.

The graphs are for the following localities, approximate, altitude, etc.

No.	Locality	Altitude	No. Specimens	Vegetation and Climate
1.	Las Vegas, Nev.	2020 ft.	8	Desert
2.	Provo, Utah	4500 ft.	15	"
3.	San Bernardino, Cal.	1060 ft.	10	Semi desert
4.	Hagerman, Idaho	2600 ft.	5	" "
5.	Galveston, Tex. (vicinity)	100+ ft.	130	Savanna
6.	Dodge City, Kan.	2500 ft.	69	Steppe
7.	Fayetteville, Ark.	1500 ft.	42	Deciduous forest
8.	Framingham, Mass.	200 ft.	149	" "
9.	Aweme, Manitoba	1180 ft.	73	Steppe
10.	Alamosa, Colorado	7536 ft.	7	"

The classes into which they are divided are somewhat artificial and some of the curves are divided.

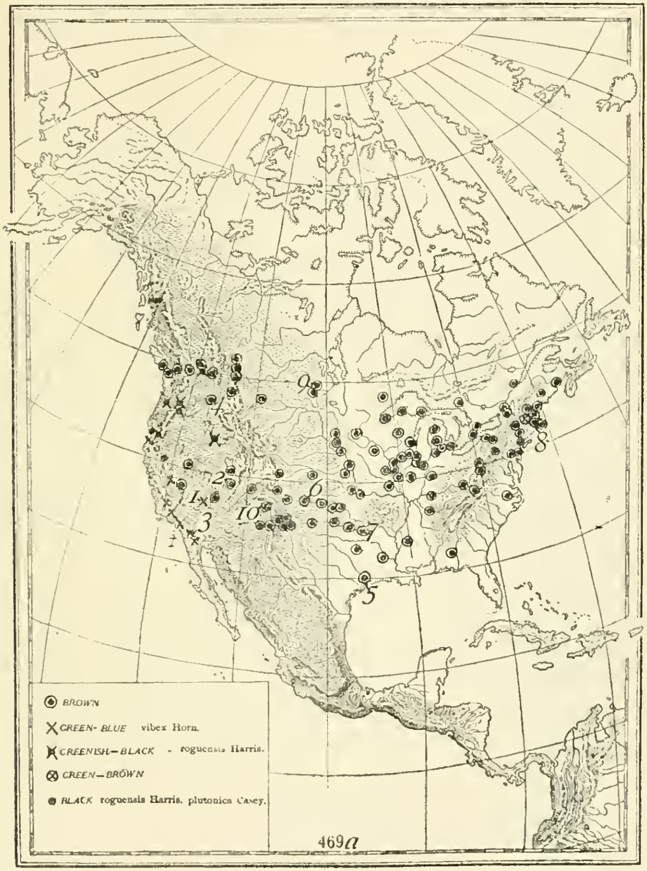


SHELFORD COLORS OF TIGER BEETLES PLATE XXI

PLATE XXII

EXPLANATION OF PLATE

FIGURE 469*a*. Showing the distribution of *C. tranquebarica* in N. America. The numbers refer to the graphs shown in figure 469. The legend shows the elytral color.


1
2
3
4
5
6
7
8
9
10
◉ BROWN
X GREEN-BLUE vibex Horn.
X GREENISH-BLACK - roguensis Harris.
⊗ GREEN-BROWN
● BLACK roguensis Harris. plutonica Casey.

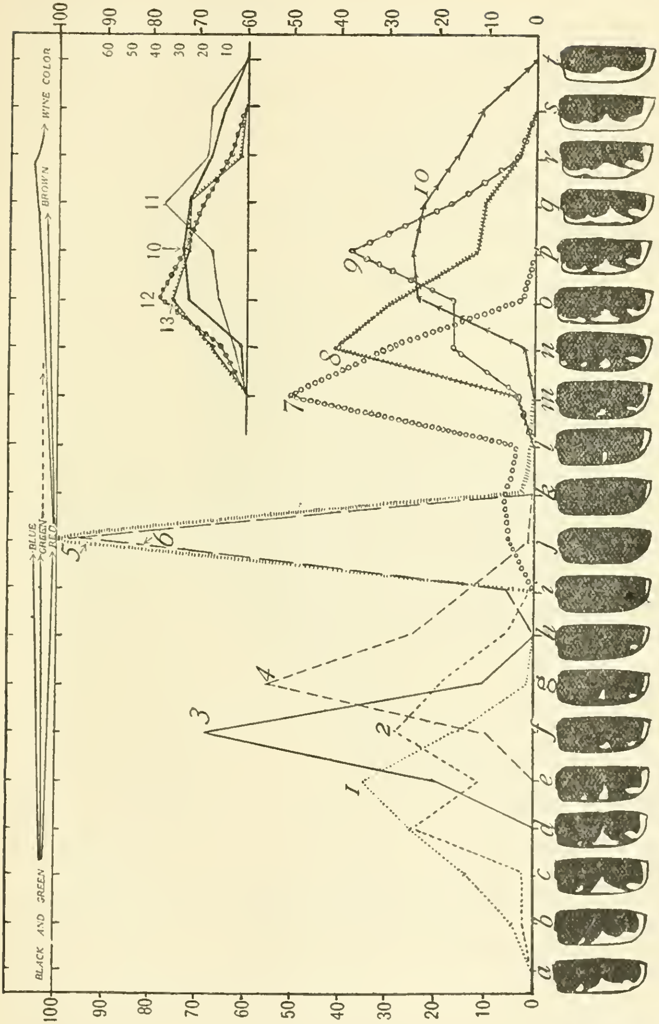
SHELFORD COLORS OF TIGER BEETLES PLATE XXII

PLATE XXIII

Explanation of Plate

Figure 470. Showing the range of variation in the group of races included under *C. scutellaris* Say. General plan as in figure 469, plate XXI. Here the individuals are arranged into classes which are strictly geographic; beginning in Massachusetts at the extreme left, they are arranged as encountered as one passes southward along the Atlantic coast and westward through the Gulf States. From Dallas, Texas, classes are arranged in order as one passes northward through western Oklahoma, Kansas, Nebraska, and South Dakota and then eastward through the Great Lakes. The classes on the extreme right (*s* and *t*) are from Aweme, Manitoba.

	Locality	No. Specimens	Generation	Collector	Altitude	Climate or Vegetation
1.	Framingham, Mass.	51	1902-1904	A. C. Frost	220 ft.	Deciduous Forest
2.	Providence, R. I.	85	1902	Bert Nock	50 ft.	" "
3.	Aqueduct, N. Y.	98	1903	L. H. Joutel	50 ft.	" "
4.	Raleigh, N. C.	59	1904	C. S. Brimley	320 ft.	" "
5.	Mobile, Ala.	20	1911	V. E. Shelford	50 ft.	" "
6.	Medora, Kan.	150	1904	"	1600 ft.	Steppe
7.	Topeka, Kan.	150	1904	"	900 ft.	Savanna
8.	Elma, Iowa	30	1902-1904	Rev. J. C. Warren	1000 ft.	"
9.	Starved Rock (Utica), Ill.	40	1905-1906	V. E. Shelford	470 ft.	"
10.	Miller, Ind.	200	1904-1905	"	600 ft.	Deciduous Forest
t.	Aweme, Man.			N. Criddle	1180 ft.	Steppe

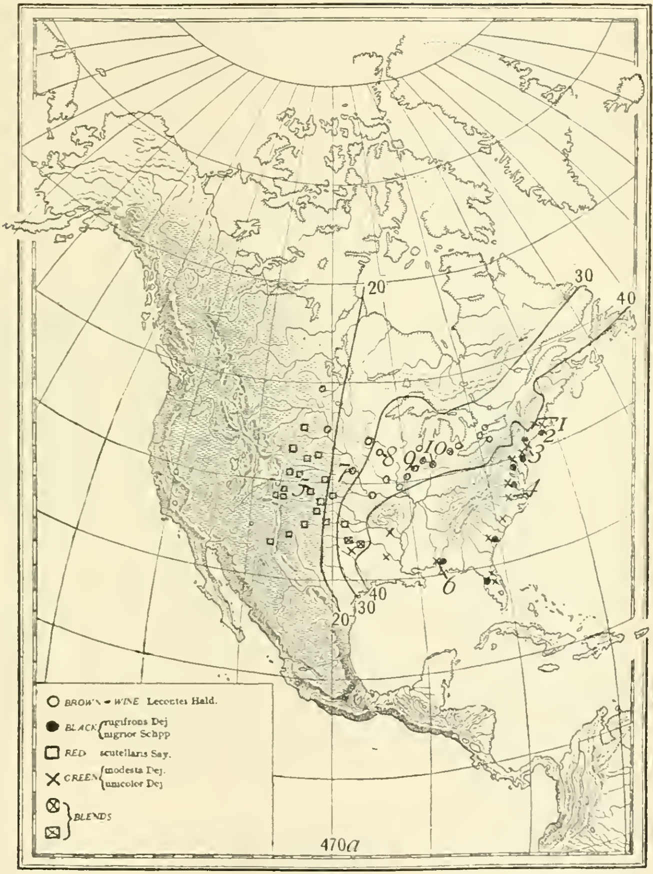


SHELFORD COLORS OF TIGER BEETLES PLATE XXIII

PLATE XXIV

Explanation of Plate

Figure 470*a*. Showing the distribution of the group of races included under *C. scutellaris* Say. The legend indicates the color of the elytron. The numbers (italics) refer to the classes of color patterns indicated in figure 470, plate XXIII. The lines and numbers indicate mean annual rainfall in inches. The mean annual rainfall to the left or west of the line designated as 20 is less than 20 inches, to the right or east more than 20 inches. To the east and south of the line designated as 30 the mean annual rainfall is more than 30 inches. To the east and south of the line designated as 40 it is more than 40 inches. Note that the colors are fairly well correlated with rainfall.


20
30
40
1
2
3
4
5
6
7
8
9
10
40
30
20
○ BROWN - WINE Lecontei Hald.
● BLACK {rugifrons Dej / nigrior Schpp
□ RED scutellaris Say.
✕ GREEN {modesta Dej. / unicolor Dej
⊗ ⊠ } BLENDS

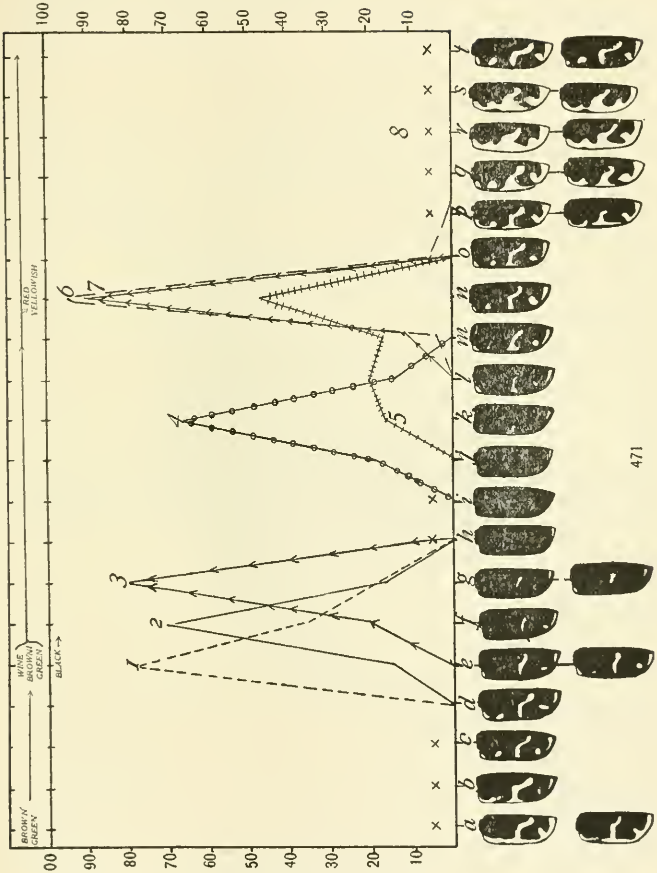
SHELFORD COLORS OF TIGER BEETLES PLATE XXIV

PLATE XXV

Explanation of Plate

Figure 471. Showing the range of variation in the group of races falling under *C. purpurea* Oliv. General plan of arrangement as in the preceding charts on other species (Pls. XXI and XXIII). In the case of this species the immaculated elytroned types which are very rare in occurrence are taken as a central type. Those to left are level ground inhabitants in which the reduction of patterns is characterized by a withdrawal of the middle band from the elytral margin. Those to the right are the steep clay bank inhabitants, except possibly class "t" (*C. decemnotata* Say); classes *a, b, c, C. cimarrona* Lec.; *d-h, C. purpurea* Oliv., *graminea* Schpp., *audobonii* Lec., *spreta* Lec. Those to the right are *splendida,* Hentz, *transversa* Leng, *denverensis* Cas., *limbalis* Klg. The graphs are for the following localities with approximate altitudes, vegetation, etc.

Locality	No. Specimens	Color or Race	Altitude	Climate or Vegetation
1. Fort Collins, Colo.	7	Green and black	5600 ft.	Steppe
2. Framingham, Mass.	128	Winecolor, brown, some greenish	100 ft.	Deciduous Forest
3. Puget Sound, Wash.	7	Green	10 ft.	Conifer
4. Kimmich, Mo.	29	*transversa*	425 ft.	Deciduous Forest
5. Topeka, Kan.	100	*splendida*	900 ft.	Savanna
6. Glencoe, Ill.	54	*limbalis*	600 ft.	"
7. Aweme, Man.	10	"	1080 ft.	Steppe
8. Sedalia, Colo.	....	Red Classes, p-s	5800 ft.	"

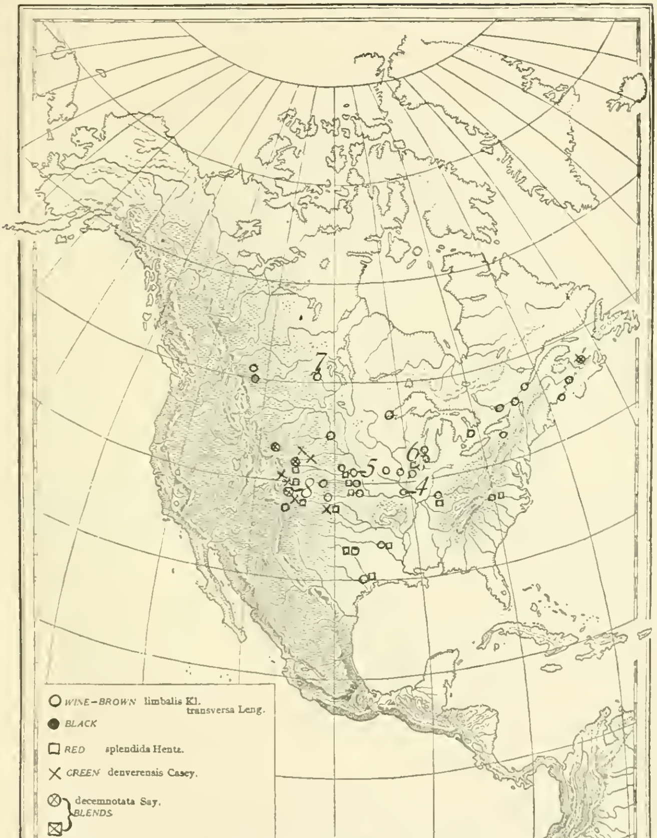


SHELFORD COLORS OF TIGER BEETLES PLATE XXV

PLATE XXVI

EXPLANATION OF PLATE

FIGURE 471*a*. Showing the distribution of the *limbalis, denverensis, transversa,* and *10 notata* races of *C. purpurea* with numbers referring to the graphs in figure 471, plate XXV, and legend showing colors.

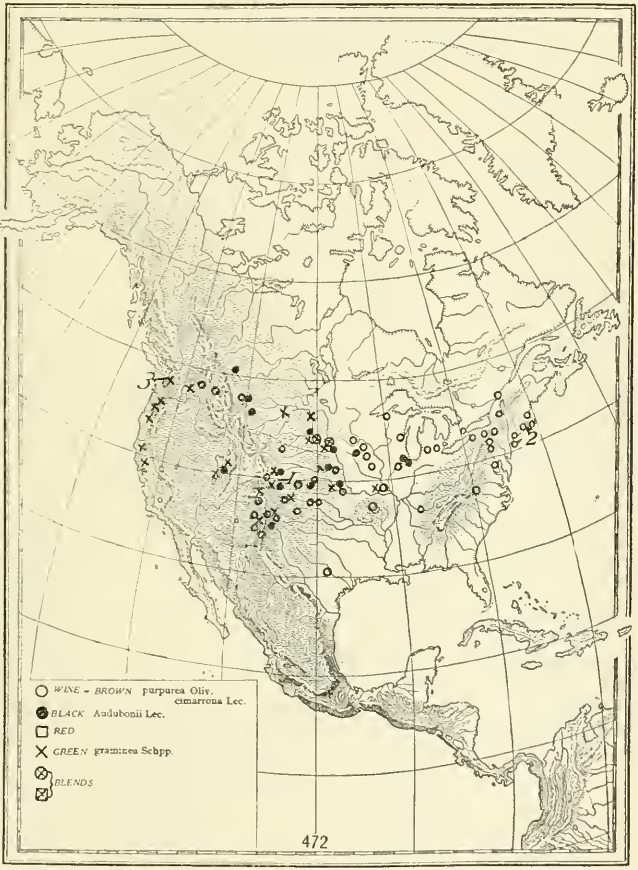

7
5
6
4
8
○ WINE-BROWN limbalis Kl.
transversa Leng.
● BLACK
☐ RED splendida Hentz.
× GREEN denverensis Casey.
⊗ decemnotata Say.
BLENDS
☒

SHELFORD COLORS OF TIGER BEETLES PLATE XXVI

PLATE XXVII

Explanation of Plate

Figure 472. Showing the distribution of the *purpurea, graminea, audobonii,* and *cimarrona* races of *C. purpurea* with numbers referring to the graphs on figure 471, plate XXV, and legend showing colors.


○ WINE - BROWN purpurea Oliv. cimarrona Lec.
● BLACK Audubonii Lec.
☐ RED
X GREEN graminea Schpp.
⊗ ⊠ BLENDS
1
2
3

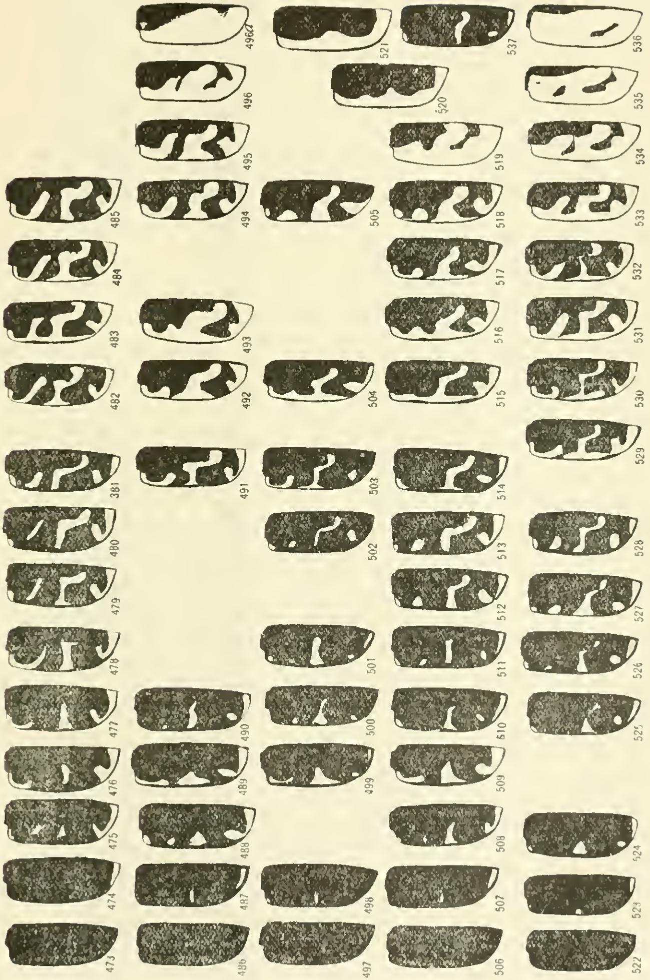
SHELFORD COLORS OF TIGER BEETLES PLATE XXVII

PLATE XXVIII

Showing the parallelism of patterns of the north stem of W. Horn's phylogeny, and *C. sexguttata* Fabr. Compare the rows with one another.

EXPLANATION OF PLATE

Figs. 473-474, *tranquebarica* Herbst subsp. *plutonica* Cas. (California) drawn from descriptions by Leng; 475-478, do. subsp. *vibex* Horn (Las Vegas, Nev.); 479, do. (San Bernardino, Cal.); 480, greenish brown form of *tranquebarica* (Hagerman, Idaho) (*roguensis* Harris); 481, *tenuicincta* Sch. (Salt Lake); 482, *tranquebarica* (Framingham, Mass); 483, *tenuicincta* Schpp. (Saltair, Utah); 484, *tranquebarica* Herbst (Alamosa, Colo.); 485, do. (Las Vegas, Nev.); 486-490, *scutellaris* Say, varieties—see figure 468 and description; 491, *echo* Cas. (Great Salt Lake); 492, *willistoni* Lec. (Lake Como, Wyo.); 492, *fulgida* Say (Kansas); 494-496, *latesignata* Lec. (San Diego, Cal.); 497-501, *pulchra* Say (499-501—Alpine, Texas, drawing supplied by Prof. H. F. Wickham, from specimens in his collection); 502, *latesignata* aber. *tenuicincta* Blaisdell (Saltair, Utah); 503-505, *longilabris* Say, varieties; 504-505, (N. Mexico); 506-518, *purpurea* Oliv., varieties (see Fig. 470); 508-509, 516-518 (Sedalia, Colo.); 519, *generosa* subsp. *mantoba* Leng.; 522-523, *sexguttata* (Onaga, Kansas); 524, do. (Chicago); 525-526, do. (Woods Holl.); 527, *sexguttata* subsp. *patruela* Dej. (Lakehurst, N. J.); 528, *12 guttata* Dej. (Chicago); 529, *ancosisconensis* Harris; 530, *repanda* Dej. (Chicago); 531-532, *generosa* Dej.; 531, do. (Framingham, Mass.); 532, do. (Lakehurst, N. J.); 533-534, *venusta* Lec. (Aweme, Man.); 535-536, *limbata* Say (Aweme, Man.); 536, *purpurea,* showing reduced and shortened marking.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SHELFORD COLORS OF TIGER BEETLES PLATE XXVIII

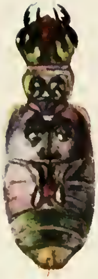
PLATE XXIX

Showing Development and General Modification of Colors in Experiments in *C. scutellaris lecontei* Hald.

Explanation of Plate

Figs. 538-542. Development of color in the ventral side.
- 538. 4 hours after emergence.
- 539. 10 hours after emergence.
- 540. 11 hours after emergence.
- 541. 15 hours after emergence—adult coloration.
- 542. Adult coloration in a dark individual.

Figs. 543-549. Color development and color changes in an individual of C *lecontei.*
- 543. 1 hour after emergence.
- 544. 11 hours after emergence.
- 545. 13 hours after emergence; compare with 553.
- 546. 15 hours after emergence.
- 547. 3 to 15 days after emergence; drawn at end of third day.
- 548. 42 days after emergence.
- 549. 85 days after emergence.
- 550. *C. lecontei,* color of modal class, Miller, Ind., April, 1906.
- 551. *C. lecontei,* Miller, Ind., June, 1906.
- 552. *C. lecontei,* color of modal class, Miller, Ind., April, 1905.
- 553. *C. scutellaris rugifrons,* typical specimen, Raleigh, N. C.
- 554. *C. scutellaris,* typical specimen, Topeka, Kansas (not modal class).
- 555. *C. lecontei,* larvae subjected to hot dry conditions during prepupal and pupal stages, note reduced markings and color—compare with normal ontogeny series above (Experiment 63); mean temperature 37°; dry; compare with 554 and 553.
- 556. *C. lecontei,* larvae forced by high temperature and brought through without hibernation (Experiment 59*a*; mean temperature 37° C.; moist.
- 557. *C. lecontei* modified by cold conditions during the pupal stage; (Experiment 65); mean temperature, 12° C.; moist. Note dull color and peculiarities of markings.
- 558. Peculiar individual from Starved Rock (Utica), Ill., showing the tendency for all the highly colored species to produce purple forms occasionally. This type occurs at Utica on the coarse sands.



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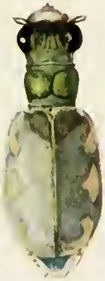

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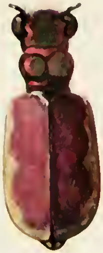

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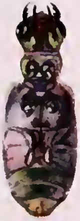
PLATE XXIX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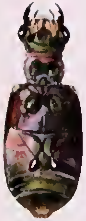
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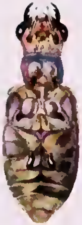
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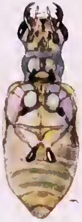
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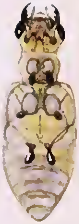
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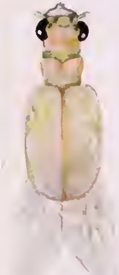
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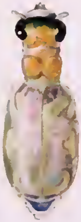
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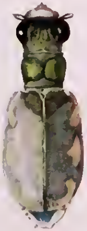
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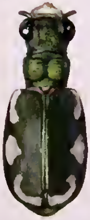
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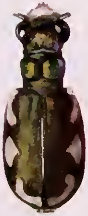
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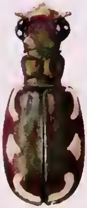
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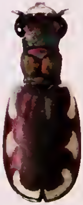
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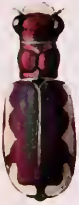
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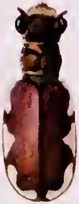
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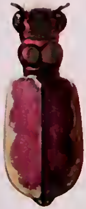
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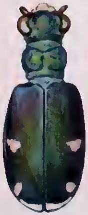
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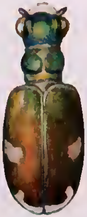
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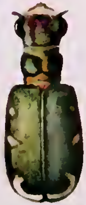
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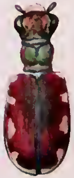
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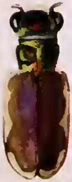
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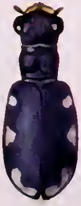
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PLATE XXX

Showing Color Development and General Modification in Experiments on Species Named.

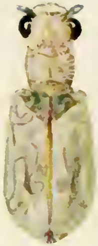
Explanation of Plate

Figs. 559-562. Color development in *Cicindela hirticollis.*
- 559. Condition 4 hours after emergence.
- 560. Condition 15 hours after emergence.
- 561. Condition 21 hours after emergence.
- 562. Condition 21 days after emergence, full adult color.

Figs. 563-565. Color development in *C. purpurea.*
- 563. Condition 20 hours after emergence.
- 564. Condition 4 days after emergence.
- 565. The same specimen as in figure 6, killed and dried on the fourth day after emergence.

Figs. 565-570. Experimental modification of color and color pattern by conditions during the prepupal and pupal stages.
- 566. Dwarfed specimen of *C. hirticollis* produced by forcing the larvae without hibernation in their last winter (Experiment 70); mean temperature, 37° C.; moist.
- 567. Normal individual of *C. tranquebarica,* collected in the field.
- 568. Specimen with color modified by being kept in an ice box, during the pupal stage, like variety in eastern mountains (Experiment 65*a*); mean temperature, 12° C.; moist.
- 569. Specimen with both pattern and color modified by hot dry conditions (Experiment 60); mean temperature, 37° C.; dry. Like variety in the western states.
- 570. Specimen with both pattern and color modified by hot wet conditions, like variety in the moist southern states (Experiment 56); 37° C.; moist.

PLATE XXX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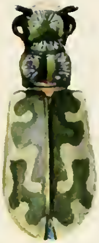
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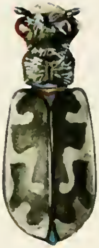
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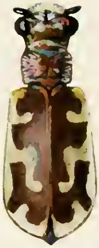
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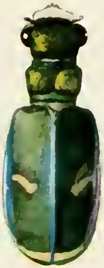
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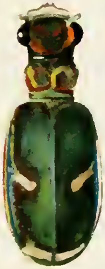
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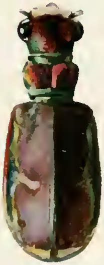
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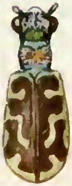
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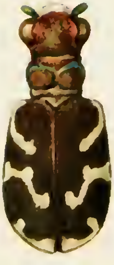
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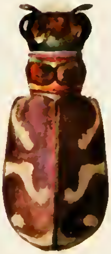
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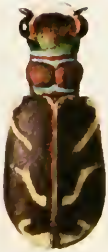
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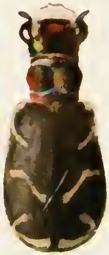
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PLATE XXXI

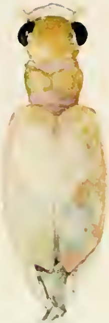
Showing Color Development and General Modification in Experiments on *C. purpurea* subsp. *limbalis.*

EXPLANATION OF PLATE

Figs. 571-574. Color development in *C. purpurea* subsp. *limbalis.*

571. Condition at emergence.
572. Condition 12 hours after emergence.
573. Condition 34 hours after emergence.
574. Condition 15 days after emergence.
575. Normal collected individual.
576. Specimen killed and dried when at stage shown in figure 573.
577. Experimentally modified individual, in hot dry conditions during prepupal and pupal stages. Resembles specimens from eastern Kansas.
578. Specimen with color modified by being kept in an ice box during the pupal stage (Experiment 65*b*); mean temperature, 12° C.; moist.
579. Specimen modified by hot moist conditions during the prepupal and pupal stage (Experiment 61); mean temperature, 37° C.; moist.

PLATE XXXI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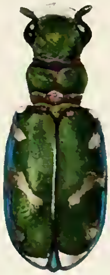
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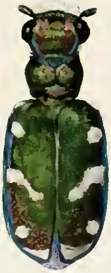
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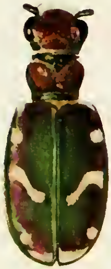
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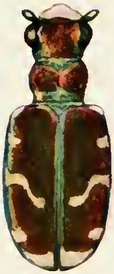
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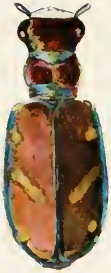
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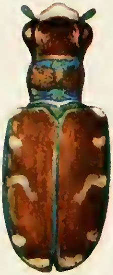
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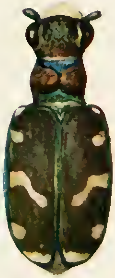
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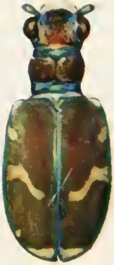
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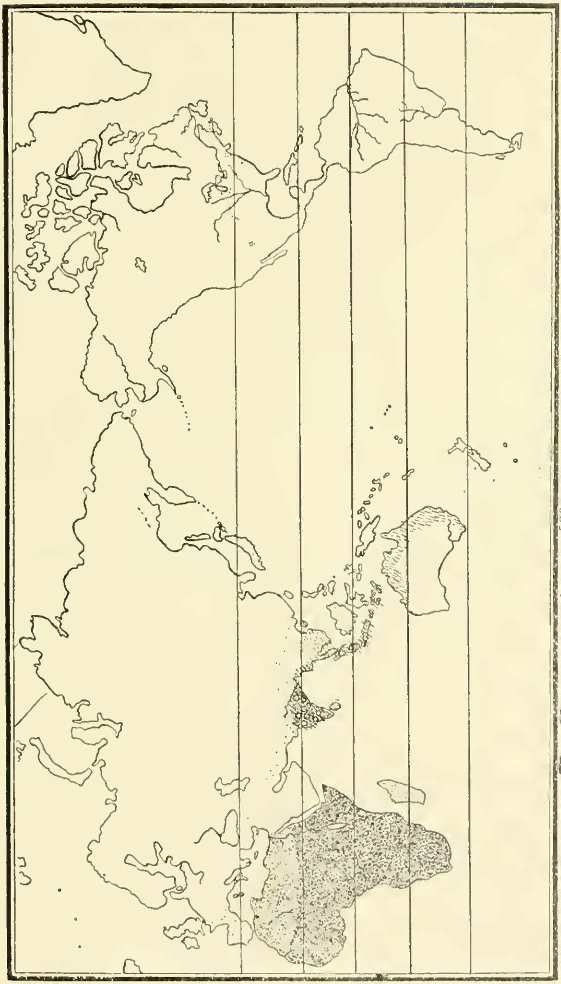
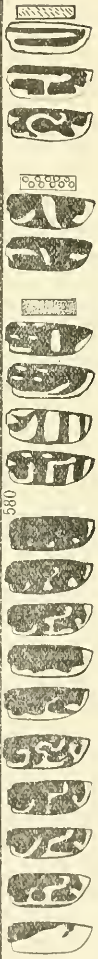
PLATE XXXII

EXPLANATION OF PLATE

FIGURE 580. Showing the geographic distribution of types and patterns. The first series at the left are world-wide in distribution, being most generalized in Eurasia and North America. The second group of patterns belong to several groups of species but all are characterized by the presence of three spots at the base and along the elytral suture. They are most numerous in Africa and India. The next group shows the relatively rare type with the pattern oblique but in the opposite direction from the slope of the tip of the elytron. The last type is one showing peculiar joinings of markings characteristic of species found chiefly in Indo-Australian region.





SHELFORD COLORS OF TIGER BEETLES PLATE XXXII

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